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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE
MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE,
E. L. MARK, DIRECTOR. — No. 185.

*AN EXPERIMENTAL STUDY OF THE IMAGE-
FORMING POWERS OF VARIOUS
TYPES OF EYES.*

BY LEON J. COLE.



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TABLE OF CONTENTS.

	PAGE
I. Introduction	335
II. Description of Apparatus	340
III. Experiments	347
1. Earthworm (<i>Allolobophora foetida</i> [Sav.]	350
2. Land planarian (<i>Bipalium kewense</i> Moseley)	361
3. Mealworm (larva of <i>Tenebrio molitor</i> Linn.)	367
4. Sow bug (<i>Oniscus asellus</i> Linn.)	371
5. Cockroach (<i>Periplaneta americana</i> Linn.)	375
6. Mourning-cloak butterfly (<i>Vanessa antiopa</i> Linn.)	380
7. Water scorpion (<i>Ranatra fusca</i> Pal. B.)	382
8. Pomace fly (<i>Drosophila ampelophila</i> Loew)	388
9. Garden snail of Europe (<i>Helix pomatia</i> Linn.)	390
10. European garden slug (<i>Limax maximus</i> Linn)	391
11. Cricket frog (<i>Acris gryllus</i> Le Conte)	392
12. Green frog (<i>Rana clamata</i> Daudin)	400
IV. General considerations and discussion	402
V. Summary	412
VI. Bibliography	415

“Die wirkliche Naturwissenschaft begann damit, dass man, anstatt über das Wesen der Schwerkraft zu fabuliren, die näheren Umstände der Bewegung des fallenden Steines, des Pendels u. s. f. genau bestimmte und möglichst genau und einfach beschrieb. In der Biologie, speziell in Bezug auf die uns hier interessirenden *mechanischen* Lichtwirkungen kann die Aufgabe des Forschers auch nur darin bestehen, die durch das Licht ausgelösten thierischen Bewegungen ihrer Abhängigkeit nach näher zu bestimmen und zu beschreiben.” (Loeb, '90, p. 20.)

I. INTRODUCTION.

THE structure of eyes has been long and carefully studied, both as to gross anatomy and finest histological detail. This is especially true

of the human eye, but the eyes of other vertebrates, and of the invertebrates as well, have received a large share of attention. The ability of various eyes to form more or less accurate images of external objects has been for the most part inferred from the application of physical laws to the knowledge of their structure. In the case of man, however, there is less need for inference, since his common experience in seeing is a constant demonstration of the ability of his eyes to form images. Nevertheless, even here certain factors which add to the efficiency of the eye as a visual organ, but are in no way concerned with the actual physical formation of the image on the retina, must be taken into account. For example, judgments based upon experience involving other elements than mere image-formation, such as the mental superposition of the images of the two eyes, giving a stereoscopic effect, the action of the ciliary muscles and other mechanisms for accommodation, and the influence of other senses, especially that of touch. The filling out of the blind spot of the retina by the mind is a good example of the influence of experience upon the interpretation of the actual sense impression. It is not unlikely that the eye of a baby is capable of forming practically as good an image as that of an adult; but the baby lacks the experience and training of the adult which would enable it to form proper judgments, and consequently it appears to have little if any conception of distances and space relations in general.

The images formed by other eyes than the human can also in a measure be studied from direct observation. Thus the image of distant objects may be seen upon the retina of the freshly removed eye of an albino rabbit, since the absence of pigment leaves the posterior portion of the eyeball semi-transparent, and the relaxed eye is accommodated to distant vision. Or, the posterior portion of the eyeball of a pigmented eye, such as that of a frog, may be cut away, and by aid of a microscope the image may be projected so that it can be observed directly, or thrown upon a screen. This has likewise been accomplished with the eyes of some invertebrates; thus Exner ('91) succeeded in taking a remarkable photograph through the eye of a fire-fly, while Parker ('95) demonstrated empirically that the compound eyes of *Astacus* form a single image rather than a number of separate images.¹ Again, in the eyes of many vertebrates the decolorizing effect of light upon the visual purple, after protracted exposure, may be seen upon the retina,

¹ The multiple photographs obtained through the corneal facets of insect eyes do not represent the retinal image formed by these eyes, since in obtaining such photographs only one portion of the dioptric apparatus is used.

and the monochromatic image thus formed may even be permanently fixed by a proper treatment with alum solution (Kühne, '79, p. 299) or platinum chloride (Stern, : 05).

By means of the ophthalmometer and other optical appliances, Beer has made an extensive study of accommodation in the eyes of the lower vertebrates and cephalopods. This faculty of accommodation may in a general way be related to image formation, since it is probable that an eye that is capable of accommodating differently to near and to distant objects must be able to form fairly distinct images of those objects. The converse, however, is not necessarily true, since there are eyes which appear to have considerable image-forming power, but show no mechanism for accommodation. The evidence that the compound eyes of insects can accommodate seems insufficient, and there is no evidence of this power in the eyes of any of the other invertebrates except the cephalopods, unless perhaps the movements of the eyes of certain copepods may be considered as such.

All the methods which have been enumerated for determining the exact nature of the images formed by eyes have certain obvious defects. Especially is this true in the more lowly organized types of eyes, where comparisons with the human eye cannot be so closely drawn. A study of structure alone cannot give an exact basis for this determination, since it is not always easy to interpret the optical properties merely from the structure. This is well illustrated in the variety of opinions that have existed as to "mosaic" vision in insects and other animals with so-called compound eyes. Empirical tests with fresh eyes lose much of their value on account of the changes that take place in the tissues immediately their blood supply is cut off and they are removed from the animal. The most serious of these changes are loss of tonus and coagulation of the fluids. The image on the retina, due to the change in the visual purple, is not definite enough to be of much use for settling this question; and the inferences to be drawn from the action of the eye in accommodation can be of only the most general nature.

It has not been the purpose of the work described in the following pages to furnish a more exact method of determining the precise image-forming powers of eyes. The aim has been, rather, to treat the formation of images from the point of view of their relation to the animal as a living organism, — to determine in what way the ability to form a more or less perfect image affects the responses of the animal to light, and what relation, if any, this result has to the normal habits of the creature, and to its behavior under experimental conditions. This investigation was suggested to me by Professor G. H. Parker, the suggestion being an outcome of his study of the phototropism of the mourn-

ing-cloak butterfly, in the course of which he found that this insect is able to discriminate between light derived from a large luminous area and that from a small one, even when the light from the two sources is of equal intensity as it falls on the animal, and that it usually flies toward the larger areas of light. He took the biological significance of this reaction to be that "this species remains in flight near the ground because it reacts positively to large patches of bright sunlight rather than to small ones, even though the latter, as in the case of the sun, may be much more intense." (Parker, :03, p. 467.) It is evident that such a reaction as that described can be taken as a rough measure of the image-forming capacity of the eyes of the butterfly studied, but a comparison of different animals on this basis can be made only in a very broad and general way.

Except for the work of Parker just mentioned, there appear to be few if any direct references in the literature to experiments or observations calculated to determine the difference in the reactions of animals to luminous (or illuminated) fields of different sizes; at least, few if any in which other factors, such as intensity and color of light, have been eliminated. An experiment performed by Loeb ('90, p. 47, Versuch 2) upon a species of crepuscular moth (*Sphinx euphorbiae*) perhaps comes closest to the conditions of the present investigation. Specimens of the moth were brought into a room illuminated at one side by a window, while upon the opposite wall was placed a kerosene lamp. Here, then, were conditions with a large area of light at one side and a small source of light at the other. No comparison was made of the relative intensities of the lights, but as the experiment was performed at the approach of twilight it is to be presumed that the light from the window was much less intense than it would have been in the middle of the day, so that the light from the lamp was relatively more intense. Animals liberated at a point midway between the window and the lamp flew to the window; and it was not until they were brought within about a meter of the lamp that they flew in its direction. Loeb regards this result as due entirely to the relative intensities of the light received from the two sources; but from the experiments to be described later, it will be seen that the larger area of the window was undoubtedly an important factor irrespective of, or at least in addition to, the intensity of the light.

A number of observations have been made on the tendency of animals to go toward, and to collect in, shaded areas. Mitsukuri observed that certain Japanese marine snails (species of *Littorina*) gathered in largest numbers in the shadow of certain objects which he used in his experiments (Mitsukuri, :01, p. 1, Experiment 2), and he furthermore

explained the movement of these snails landward at the time of flood tide, when they are negatively phototropic, as due to the fact that, on account of the bank, with bushes, grass, rocks, etc., less light came from that side. Somewhat similar observations have recently been made upon another species of *Littorina* (*L. rudis*) by Bohn (:05), who found that snails moving in an illuminated field took a course determined by the relative amount of light coming from different directions, and that if black or white vertical screens were placed in the field, the course of the animals was correspondingly deflected; they were "attracted" or "repulsed" by the screens, as the case might be. Bohn emphasizes the importance of the size of the screen, but makes no attempt to determine whether the greater influence of a large screen is due to the formation of a correspondingly larger image upon the animal's retina or merely to the fact that it reflects a greater amount of light if it is white, and absorbs more if it is black. He apparently made no attempt to determine exactly his light intensities, either absolute or relative, and consequently his results are rather crude and only qualitative in this respect.

Torelle (:03, pp. 470, 471) made a number of tests of frogs with reference to shadows and to dark objects, and found that, although ordinarily positively phototropic, they move out of the sunlight into the shadow, even when by so doing the movement is away from, or at right angles to, the direction of the ray (p. 487). When once in the shadow, however, the animals turned and faced the sun-illuminated area. This occurred when the shadow was that of a building or merely that beneath a box raised a short distance from the ground. These results in their bearings upon the present investigation will be discussed more fully in considering the results of my own experiments.

The greater part of my experimental work consisted in testing the reactions of various suitable animals to two sources of light, differing in area, but of equal intensity at a point midway between them, where the animals were exposed. It was planned so far as possible to select animals with representative types of eyes, such as direction eyes (planarians, etc.), compound or mosaic eyes (insects, crustaceans, etc.), and camera eyes (vertebrates), and, in addition, to conduct parallel experiments upon eyeless forms (such as the earthworm) which are known to be sensitive to photic stimulation. For the purpose of the experiments it was obviously necessary to use only animals which were decidedly positive or negative in their reactions to light, since those which were normally irresponsive or indifferent to light coming from one direction only could not be expected to show evidence of discriminating between luminous areas of different size. Furthermore, in so far as possible,

animals which normally react positively to light, and also those which are negative, were used in order to determine whether, as would be expected *a priori*, the responses (evidences of discrimination between the two lights) were reciprocal in the two cases. Forms which would require to be experimented with under water were avoided on account of the practical difficulties involved, — not only optical complications due to the reflection and refraction of light by the water and the containing vessel, but also on account of the difficulty of directly testing the lights at the middle point in order to determine whether that received from one source was exactly equal to that received from the other.

Before passing on to a description of the apparatus most used, I wish to express my indebtedness to Professor G. H. Parker, to whom, as has already been mentioned, the study owed its inception, and under whose direction, in connection with one of his courses, it was carried on for a year. The later prosecution of the work was under the direction of Professor E. L. Mark; to him I owe my gratitude for much valuable criticism and advice, since to his attention to accuracy of method both in experimentation and in the deduction of conclusions therefrom must depend in large part any merit which the present contribution may possess.

II. DESCRIPTION OF APPARATUS.

In all the experiments on the reactions of animals to two lights of different areas, as well as in certain of the other lines of investigation, the same general apparatus was used. Special devices were found necessary in working with each species of animal; these can best be explained in connection with the accounts of experiments with the respective species. Although the apparatus was changed in some of its details and added to from time to time, the changes and additions were small and comparatively unimportant, the general plan and arrangement of the apparatus remaining essentially the same throughout. It will be described in its final form, reference being made to such additions or alterations as seem to be worthy of mention.

The apparatus was installed in a long, narrow room (7 meters by about 2 meters) commonly used for photographic purposes. The single window of this room could conveniently be made light tight, while an antechamber at the entrance provided against the admission of stray light at that end of the room. The side walls were of brick, the roughness of which tended to give less definite reflections than smoother surfaces would have done, and the whole interior of the room was painted dead black. Furthermore, practically everything in the room

which did not from its nature need to be otherwise was painted black to prevent the reflection of light.

The definite arrangement and relation of the parts of the apparatus as viewed in vertical elevation may be seen in Figure 1, while Figure 2 shows the horizontal plan. Against the north wall of the room was placed a large wood-top table (*T*); at the right of this a lamp (*Sm*), giving as nearly as practicable a point of light; and at the left, at an equal distance from its centre, the apparatus (*Lg*, *Lg'*) designed to furnish the larger illuminated area (*g*). A third lamp (*V*) was placed directly above the middle point of the line joining the other two lights,² a line which may be designated as the *directive axis* (*a*, Figure 2).

The lamp giving the small light (*Sm*) consisted of a wooden box ($22 \times 22 \times 35$ cm.) painted black, and having a Nernst filament arranged before a small opening in the side facing the table. By this arrangement a definite and clear-cut luminous area was secured. Since there was no reflecting surface immediately back of the filament, the light given off in that direction traversed the blackened box and was absorbed by the distant walls, two of which were set at an angle to each other, as shown in Figure 1, to prevent, as far as possible, reflection of light.

The filament used on this lamp was the regular 110-volt "single glower" Nernst filament, which is about 15 mm. long and has a diameter of approximately 1 mm.

The illuminating apparatus (*Lg* and *Lg'*) furnishing the large light was more complicated. The lamp proper (*Lg'*) was similar to *Sm*, except that two 220-volt "six glower" filaments were used on a circuit of the strength indicated.³ The light of these two filaments was many times stronger than that of the small lamp. In front of the lamp *Lg'* was a long box (*Lg*), lined throughout with white glazed paper, except the end nearer the table, which was closed with a plate of ground glass (*g*). The end farthest from the table made an angle of 45° with the sides of the box (see Figure 2). An opening (*o*) in the side of the box near the end farthest from the table admitted the light from the lamp *Lg'*, which fell at an angle of 45° upon the white paper covering

² The word "lights" is here used to designate the luminous areas which furnished the light used in the experiments. In the case of the lamps *Sm* and *V*, these were Nernst filaments used directly; in the case of *Lg* it was a large square of ground glass illuminated by light from behind. The lamp *V* was not used in the experiments described in the present paper.

³ The 220-volt current was secured by using a transformer on the same (110-volt) circuit that supplied the smaller lamp.

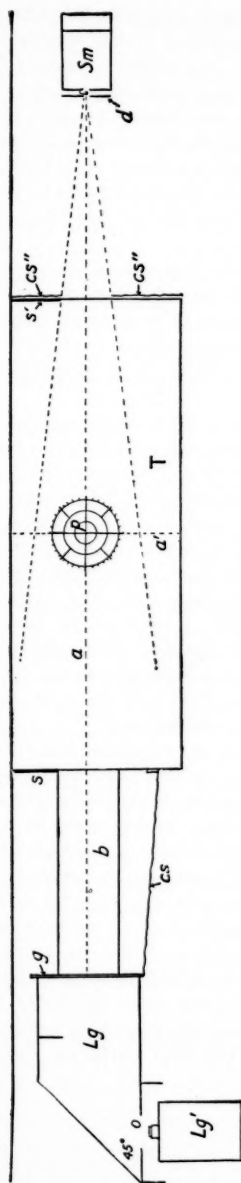


FIGURE 2.

FIGURES 1 and 2. General scheme of apparatus. Figure 1, elevation; Figure 2, plan: a , directive axis; a' , normal axis; b , board connecting table tops; cs , cs' , cloth screens; d , d' , diaphragms; g , ground glass; Lg , box of apparatus furnishing large luminous area; Lg' , lamp shining into interior of Lg through o , an opening in the side of Lg ; p , working position; Sm , lamp giving small area of illumination; T , table; V , lamp designed to throw light down vertically.

the oblique end of the box, and was thus reflected directly toward the ground glass. The white-paper lining of the sides aided in securing the desired diffusion of light. In this way a remarkably even illumination of the large sheet of ground glass was obtained. By means of a square mat of opaque paper a clear field 41 cm. square was produced, and this constituted the larger of the two areas of illumination used in the experiments. The ground glass was first placed with the unground surface toward the table, but later the ground side was turned in that direction, in order to avoid the reflection of light from the small lamp opposite.

The lamp (V), sending down vertical rays, was essentially like the small lamp (Sm), being similarly provided with a single 110-volt filament. There was arranged in front of it, however, a sliding diaphragm (not shown in the figure), by means of which the size of the orifice, and therefore the amount of light coming from it, could be regulated at will.

The filament of the small lamp (Sm) and the ground glass (g) of the large lamp (Lg) were each exactly 2 meters from the central point (p) of the table. For convenience this middle point may be spoken of as the *working point* or *working position*. All light, except that coming directly from the sources described, was excluded, as far as possible, from the working position by means of diaphragms (d), screens of heavy pasteboard or wood (s, s', s''), and black cloth (cs, cs', cs''). The intensity of illumination of the ground-glass surface could now be easily regulated by varying the distance of the lamp Lg' from the oblique reflecting surface in the box Lg . With the aid of a Lummer-Brodhun photometer placed at the working position (p) it was an easy matter, by varying the distance from o of the light Lg' , to make the intensities of the two lights exactly the same.

It is now necessary to compare the respective areas of the two sources of illumination. The small filament was 1 mm. in diameter and 15 mm. long, but at each end was a small knob where the platinum wires were attached to the filament, and when the latter was at white heat these glowed as well. Thus the total length of glowing surface was about 17 mm. Since the illuminated surface of the ground glass was 41 cm. square, as has been stated, its area was 168,100 sq. mm. If in the small lamp we regard the filament only, we shall have an area of 15 sq. mm., and therefore the ratio of the two areas will be that of 11,207 to 1. If, however, the length of the smaller light is considered as 17 mm., the ratio becomes 9,888 to 1. Since the ratio cannot be obtained with great accuracy, and the exact proportion is of only minor importance, we may, for all practical purposes, regard the ratio as 10,000 to 1.

The intensity of the light from either source was found at the end of the investigations to be only about 1.25 candle meters. There were two reasons why this intensity was not constant throughout the experiments. In the first place, the voltage appeared at times to be very inconstant, causing considerable fluctuation in the intensity of the lights. These fluctuations were usually of sufficient amount to be noticeable; but since both lights were on the same circuit, the *relative* intensities were but little affected; however, at such times the lights were tested with the photometer, in order to make sure that they had not changed relatively, and that they were still balanced at the working point. It was found by experience that with small fluctuations their change in relative intensity was inappreciable, it being only in cases of considerable fluctuations that it was necessary to make any readjustment. The other change in intensity was due to a gradual deterioration of the filaments, and therefore was more constant. The light intensity employed at the beginning of the investigation was very close to 5 candle meters, from which, as stated above, it gradually ran down to as little as 1.25 candle meters in the later experiments. The whole change from this cause was probably not so great, however, as sometimes occurred in the temporary fluctuations due to varying voltage. We seem justified in leaving these comparatively small inconstancies out of consideration, since it is not probable that they were of sufficient amount to influence materially the results on any of the animals used. At most, these differences could probably have made only a slight difference in the percentage of reactions and none in their character, since Adams (:03) has shown that in the earthworm, for example, it is only at very low intensities, near the point where the animal changes from negative responses to positive, that small differences of intensity have a relatively great effect. At the higher intensities considerable range in the intensity produces relatively little change in the percentage of responses. Furthermore, the animals employed in these experiments were selected for their decided reactions to light of about the intensity used, and it is probable that in no case where positive results were obtained was this near the point where these forms change the character of their response.⁴

By means of a microspectral photometer the qualities of the two lights

⁴ The common European garden snail (*Helix pomatia*) was found to be so inconstant in its responses that it was not suitable for the purpose of these investigations. This may have been because the light used was near the *critical intensity* for this species, though it is more probable that the changes in response depended entirely upon certain physiological states of the animal independent of the light (see p. 391).

were also tested and compared. The differences in the spectral components were found to be so slight as to be negligible. A sheet of clear glass, equal in thickness to the ground glass of the large light, was at first placed in front of the small light, in order to make the conditions of the two as similar as possible; but it was found to be of little use, and was of such obvious disadvantage, because of the considerable dispersal and reflection of the light which it caused, that it was later dispensed with entirely, and consequently is not represented in the figures of the apparatus.

The vertical light (V), which has been described, was used only in connection with the small light (Sm) in studying chiefly the reactions of animals to lights of equal intensity, but coming from different directions, — in this case one light striking the animal from directly above, the other coming to it horizontally. This combination of lights was also employed in studying the reactions to shadows and to sudden differences of intensity. These experiments will be described in another paper.

Other appliances and conveniences will be mentioned in their proper places. It should be stated here, however, that screens were provided by means of which the light from any of the lamps could be immediately shut off from the working position at will.

At the point on the table exactly midway between the lights was painted a white line, and this may be spoken of as the *normal axis* of the apparatus (a' , Figure 2), since it is at right angles to the directive axis already mentioned. At the beginning of each trial in an experiment the subject was usually placed, headed in one direction or the other, on this line, its long axis coinciding with the line. For the sake of brevity in description, this is called the *normal position*. Any line running parallel to the normal axis — nearer to one light or the other — may be said to run in a *normal direction*. The centre of the *working position* was at the point where the normal and directive axes crossed, and the working area included a small horizontal surface, the extent of which was determined by the distance the animals were allowed to move. Three concentric circles, the inner with a radius of 5 cm., the second with a radius of 10 cm., and the outer with a radius of 15 cm., were described with their centres at this point. Each of the circles was divided by short cross lines into arcs of 10° , and by means of this device the angles at which the animals deviated from the normal axis and crossed any of the circles could be read directly with ease and accuracy.

III. EXPERIMENTS.

As stated in the Introduction, the experiments were undertaken with the idea of ascertaining, as far as possible, to what extent complexity in the organization of eyes is correlated with the reactions to luminous areas of different size but of equal total luminosity. The character and relative percentage of phototropic responses were used as measures of the reactions. The method employed can perhaps best be explained by an example. Let us suppose that an animal which is decidedly positive in its ordinary reactions to directive light is placed midway between two luminous areas of exactly equal shape, size, and intensity, and in such a position that one light is at its right, the other at its left. Let us assume, further, that each luminous area is 1 cm. square, has an intensity of 100 c. p., and is situated at a distance of 2 meters from the animal. The measure of the light then impinging upon either side of the subject would be 25 C.M. (candle meters). We should expect one of two results: (1) The animal being equally stimulated upon both sides would go straight ahead without turning; or (2) owing to chance or random movement, it would become turned slightly more towards one light, which would thus have a more direct effect than the other, and the animal would then continue crawling towards this light. But since the chance of random movements in one direction is as great as in the other, the number of times that the animal would go towards each of the lights should, in a large number of trials, be equal, and we should have essentially a balanced condition as before.

Now let us enlarge one of the areas to, say, 100 cm. square, but keep the total amount of light given by it the same as before. Its area is now 10,000 times as great as before, and consequently the intensity of the light radiated from a single square centimeter is now only 0.01 c. p. The whole amount of light received by the animal is, however, the same as before, namely, 25 C.M. upon each side. If the animal is without image-forming organs, — in other words, without eyes, — it has no obvious means of appreciating the increase in size of one of the areas, and we should expect the reactions to be the same as when the lights were of equal size, that is, the animal would be indifferent. In this case, the skin (or certain scattered cells in the skin) is the sensitive surface, and since there is no apparatus for concentrating the light from the large area, the amount of light received by any point on the skin on either side of the animal is equal to that received by any other. This is evident from the fact that light from every one of the 10,000 areas (each a centimeter square) which make up the large area falls

upon each point of the surface of the animal; the intensity of the light from any single square centimeter of the area is only 0.0025 C.M., but since there are 10,000 such radiating squares the total intensity is 25 C.M.

In an animal possessing eyes capable of forming good images of external objects the conditions are very different. In this case light from all parts of the large area cannot fall upon every point in the sensitive surface (here the retina), but the light from each part of the field retains its position relative to that from other parts, and falling upon the retina in this order covers there an area similar in shape and relative intensity of illumination to the external one. Such is the image. The small light, which we are considering as only 1 cm. square, would likewise form an image on the retina, and this, with the light at the given distance, would cover a certain small area, which we may denote by x . x , then, is the size of the retinal image of a luminous object 1 cm. square at a distance of 2 meters. The light received on this area would have a certain intensity, which may be designated by y . Now, since the large light has 10,000 times the area of the smaller one, its image on the retina (making no allowance for aberration or other optical defects) would be 10,000 times as large as the image of the small light, or 10,000 x ; and the intensity on any single area x would be only $\frac{1}{10000} y$. It is obvious, therefore, that under these circumstances we have entirely different conditions of stimulation on the two sides — that is, in the two eyes — of the animal. On the retina of one eye only a very small area (x) is stimulated, but the light has a considerable intensity, which we have called y . The retina of the other eye is stimulated over a much larger area (10,000 x), but each area (x) receives in this case a light intensity of only $\frac{1}{10000} y$.

This is of course only an approximation to the relative influence of the two sources of illumination. It is probable that even in the most highly organized eyes, owing to aberration and other defects, the actual conditions are far from those here assumed. It must be remembered, furthermore, that from a physiological standpoint the retina cannot be accurately divided into areas, such as we have assumed x to be, corresponding to external areas, but that its physiological action, as well as its finer structure, must be considered in terms of visual elements — the ommatidia in the compound eye, the rods and cones in the vertebrate eye. The matter is further complicated by the fact that these visual elements may not have a uniform distribution over the whole retina, nor do we know that those of different parts of the organ are equally sensitive to light stimulation.

In spite of these defects and deviations from the suppositional case,

we are safe in assuming (1) that the image of the larger light is spread over a larger area on the retina, or better, that a larger number of visual elements receive light, and (2) that the intensity of the stimulus acting on any one visual element is very much less than that which acts on the one element, or very few elements, which are stimulated by the small light. Analogy with the reception of stimuli by sense organs in general makes the assumption reasonable that the difference between even a very weak light and no light falling on a visual element may have a much more stimulating effect upon the animal than the same, or even a greater, difference in the amount of the light at higher intensities. Such being the case, we should expect an animal to react more strongly to that stimulus which fell upon the larger number of visual elements — that an animal normally positive, for example, would be more strongly positive to the large light than to the small, and similarly that a negative animal would tend more often to move away from the larger than from the smaller luminous area. Parker's (:03) results give evidence that in *Vanessa* such is really the case. In the following pages are recorded the results of experiments made under more uniform and more precisely determined conditions upon a variety of animals, some negative and others positive, some with eyes and others without.

The kinds of animals experimented upon were not taken entirely at random, but species whose reactions to a single light were definite and well known were selected as far as possible. The number of animals from which selection could be made was greatly limited owing to the optical difficulties with animals living in water. Only those were used, consequently, which could be studied in the air. In addition to the animals with which a considerable series of experiments was finally made, a large variety of animals were tested in a more or less complete manner, to determine their suitability for the work. These included a number of insects, such as the water strider (*Hygrotrechus*), an elater, a small species of cockroach, and certain kinds of bees and flies, several myriapods and spiders, the European slug (*Limax maximus*), the horned toad (*Phrynosoma*), and two species of salamanders (*Plethodon glutinosus* and *P. erythronotus*). Some of these did not appear from their movements to be responsive to light, others were inconstant in their responses, and still others were too inactive for the purposes of this work. Those from which more or less satisfactory data were obtained are as follows: 1. The common dungworm or earthworm (*Allobophora foetida* [Sav.]). 2. A large land planarian (*Bipalium kewense* Moseley). 3. The mealworm (larva of *Tenebrio molitor* Linn.). 4. The sow bug (*Oniscus asellus* Linn.). 5. The cockroach (*Periplaneta americana* Linn.). 6. The mourning-cloak butterfly (*Vanessa anti-*

opa Linn.). 7. The water scorpion (*Ranatra fusca* Pal. B.). 8. The pomace fly (*Drosophila ampelophila* Loew). 9. The common garden snail of Europe (*Helix pomatia* Linn.). 10. The cricket frog (*Acris gryllus* Le Conte), and the green frog (*Rana clamata* Daudin).

Below are set forth the results of the experiments on these animals in the order given above. The statement of results is followed by a discussion of their significance.

1. Earthworm (*Allolobophora foetida* [Sav.]).

In connection with observations upon the reactions of a series of animals having eyes of different kinds and of varying degrees of complexity, it seemed desirable, for the sake of comparison, to make similar observations upon a form without eyes. Of all the forms available, the earthworm appeared to be the best suited to this purpose. A number of observers have worked with earthworms of various genera, so that their behavior in relation to light is better known than that of many other animals. Although there appear to be differences in the degree of sensitiveness of different species, the behavior of the several kinds that have been studied seems to be essentially the same.

That earthworms ordinarily respond negatively to light of moderate intensities was early remarked by Hoffmeister ('45), and subsequently by Darwin ('81), and has been abundantly confirmed by all later workers. For the purpose of the present investigation it was sufficient that the worms react in this manner in a large percentage of cases, and that they lack eyes, — that is, any organs for focussing the light upon special sense cells. The fact that they possess such special cells as the so-called light cells, — demonstrated by Hesse ('96) and shown for Perichaeta by Harper (:05), — has no bearing in this connection, since there is no contrivance for concentrating the light upon these structures. Nor does it matter that the animal is sensitive upon all parts of its body, though to a different degree in the different regions, as shown by Parker and Arkin (:01). Indeed, it is unimportant to know in what manner the reaction is brought about; whether it is a direct response, in the sense of the tropism theory, or a result of trial and error, as maintained by Holmes (:05) and confirmed for moderate intensities of light by Harper (:05), since the problem is merely to determine, as indicated by the direction in which the animal moves, whether it is more strongly stimulated upon one side than upon the other.

Method of Experimentation. The luminous areas, as previously explained, were fixed, one at the left and one at the right of the experimentation table. Earthworms in good condition, which had previously

been kept in the dark, were tested, each in its turn, first, with the lights separately, and then with both acting at the same time. In each experiment the worm was placed in the normal position, — that is, with its long axis at right angles to the rays of light (see p. 346), — and allowed to crawl a distance of 15 cm., i. e., until its anterior end crossed the outer circle marked on the table (see p. 346, and Figure 2, p. 343). The course and the angle at which the worm crossed the circle were immediately recorded on blank diagrams differing from the table diagrams only in the absence of one of the three circles. These circles were divided, as on the table diagram, into arcs of 10° each. When the worm had been tested five times with the head started in one direction, it was then tested an equal number of times with the head started in the opposite direction. Experiments of this kind and number were made in succession with five different worms, such experiments — 50 in number — constituting a *set*. Three such sets of experiments were made, and they may be designated as *A*, *B*, and *C* respectively. Sets *B* and *C* were performed under precisely similar conditions, and may be considered together; in set *A* the conditions differed from those of sets *B* and *C* only in the method of starting the worm. This method proved to be much less satisfactory than the one employed in sets *B* and *C*.

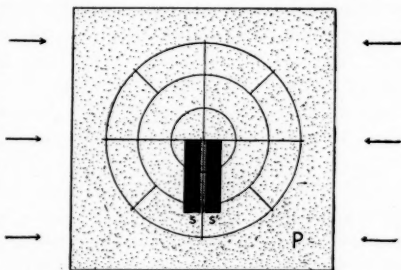


FIGURE 3. Apparatus used in earlier experiments with earthworm: *P*, ground-glass plate; *s*, *s'*, small glass strips forming runway.

In the experiments of set *A*, a ground-glass plate (Figure 3, *P*) was placed on the diagram on the table, and the worm was allowed to crawl on the roughened glass surface. The plate was kept moist by the frequent use of a damp sponge, and when thus moistened was sufficiently transparent to show the circles and radii on the table below. Two strips of thick glass (*s*, *s'*) — made opaque by being painted, except where the worm was to come in contact with them — were placed parallel to the normal axis, with one of their ends at the directive axis, and with a space between them only a little wider than the diameter of the worm's body. This formed a trough, or runway, in which the worm was placed and allowed to start crawling, whereupon a third

piece of glass was used to cover the runway. Thus, when the worm emerged from the end of the runway, its anterior end projecting out, it was subjected to the lights in the desired manner. To start the worm headed in the opposite direction, the glass strips were moved on the plate to a similar position on the other side of the directive axis.

The results of 50 trials made in this way under each condition of illumination were as follows:

a. *Response to small light alone.* In 50 trials the animal turned 43 times away from the light (— reactions) and 7 times toward it (+ reactions). This gives an excess of 36 responses away from the light, or 72 per cent of the whole number. This may be taken as a measure of the negative phototropism of the worm under the given conditions (cf. Parker and Arkin, :01, p. 153).

b. *Response to large light alone.* Out of 50 responses 3 were toward the light (+), 44 away from the light (—), and 3 straight ahead or indifferent. The excess away from the light was 41, or 82 per cent.

c. *Response to simultaneous influence of both lights.* Out of 50 trials 31 resulted in a turning towards the large light, 15 towards the small light, and 4 were indifferent. Here there is an excess of 16 reactions, or 32 per cent, away from the small light and towards the large.

This result is far from what would be expected in the case of an eyeless animal. One would suppose, since, when both lights are used, the amount of light striking the worm on each side is the same, that the responses in each direction would be much more nearly equal in number. Another noticeable fact is the high percentage of negative reactions when only a single light was used. The highest average of negative responses obtained by Adams (:03) was 59 per cent. This was observed with a light of 48 C.M. intensity at the point where the worms were placed.⁵

In this set of experiments no mention has hitherto been made of the angle at which the worms turned. It was found upon an inspection of the records that in fully a third of all the trials made the animals upon leaving the runway had turned at an angle of 90°, confirming the suspicion awakened by watching them, that their natural thigmotactic response caused them in a large number of cases to turn sharply and follow the ends of the strips of glass. For the same reason they also

⁵ It should be borne in mind that the present results are not strictly comparable with those of Parker and Arkin or of Adams, since those investigators recorded all definite head movements (i. e., crawling movements), while in these experiments the direction of the turning in an excursion of 15 cm. is used.

appeared very reluctant to leave the runway, often drawing back completely after the anterior end had been extended a centimeter or two. It was only by stimulating such individuals at the posterior end that they could be induced to continue crawling.

As it seemed possible that the factor of thigmotaxis might have vitiated in large measure the results, the second and third sets of experiments (*B*, *C*) were made under somewhat different conditions. The ground-glass plate, instead of being laid upon the table, was suspended about 2 cm. above it by means of strings leading upward to a common point, and thence to the ceiling in much the manner devised by Parker and Arkin (:01, p. 151). In this way the horizontal position

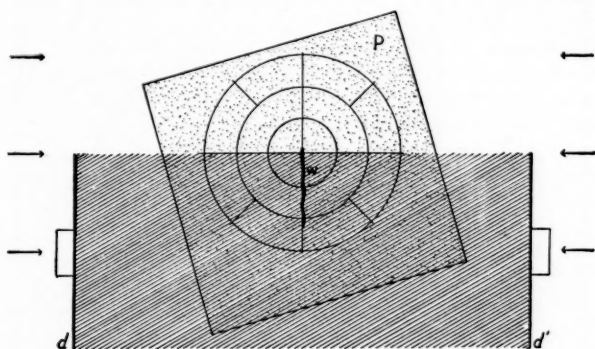


FIGURE 4. Apparatus used in later experiments with *earthworm*, and with the *land planarian*, *mealworm*, *snail*, and *slug*. *d*, *d'*, diaphragms or screens of heavy pasteboard; *P*, ground-glass plate; *w*, worm.

of the plate was maintained, but it could be moved in any direction in a practically horizontal plane, and could be rotated freely about its vertical axis. The worm could now be allowed to crawl freely on the glass plate. By means of the opaque screens *d* and *d'* (Figure 4), it was kept out of the influence of the light until it had straightened out and was moving well, whereupon, by revolving the plate if necessary, and moving it horizontally in the right direction, the worm (*w*) could be brought into the normal position, with its anterior end projecting about a centimeter beyond the directive axis, i. e., into the lighted area. In this way it crawled out into the lighted area at right angles to the direction of the rays of light, and without the disturbing thigmotactic influence of the sides of the glass runway existing in the previous experiments. When once in position, the glass plate was held station-

ary until the worm had crawled to the outer circle marked on the table, a distance of 15 cm. When it was desired to test the worm headed in the opposite direction, it was only necessary to shift the screens d and d' to the other side of the directive axis. This arrangement proved to be much more satisfactory than the one first employed, the results being free from the disturbing factor of thigmotaxis.

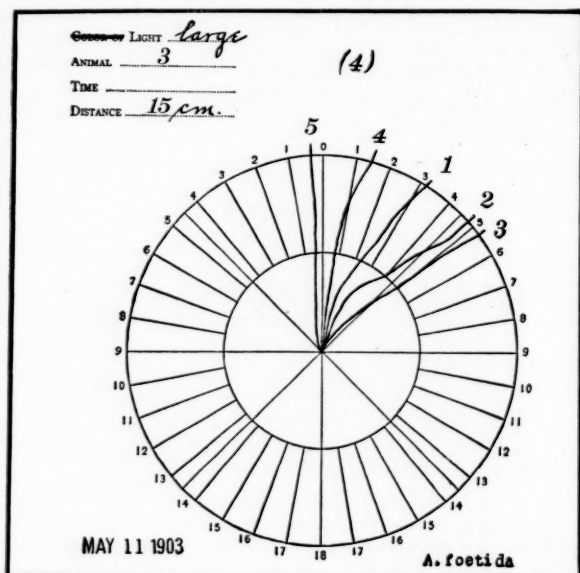


FIGURE 5. Record of five successive trials with an *earthworm* exposed to the influence of the large area of illumination and headed away from the observer. For fuller explanation see text.

The difference in the results in these two cases emphasizes the importance, in work of this nature, of bearing in mind and eliminating, as far as possible, all extraneous influences.

Before describing these experiments and their results, it may be well to describe in some detail the methods employed in keeping the records, since the same description will apply in the case of most of the animals studied. Figure 5 shows a record of five successive trials with a single worm, — in this case exposed to the influence of only one light (the one having the larger area), which was situated at the

left. The worm is in all five cases headed away from the observer. It will be noticed that the circles on this printed blank are divided into divisions of 10° each, corresponding to the divisions of the circles on the table, so that it was an easy matter to plot the path of the crawling worm with considerable accuracy. The successive trials were numbered in the order in which they were made, from one to five. When the animals were headed in the opposite direction (toward the observer), similar blanks were used, but the zero point of the transverse, or normal, axis of the circles was the near end, not the far end. By this device the relation of the lights to the diagram is kept always the same; the large light being at the left, the small light at the right.

In giving numerical value to the angles at which the outer circle was crossed, the readings were, for convenience, grouped into as many classes as there were divisions of the circle. Each class was designated by one of the numbers, 0 to 18, and embraced all the records falling within 5° of the radius bearing the corresponding number. Its nature was further indicated by *Lg* or *Sm*, according as the radius in question lay on the side of the normal axis toward the large light or toward the small one. The dividing lines (radii) shown on the diagram therefore fall in the middle of their respective classes; thus, for example, the radius numbered 2, which marks a point 20° from the normal axis, is in the middle of class *Lg* 2, or *Sm* 2, as the case may be, and all crossings between 15° and 25° fall in this class. Crossings which happen to lie exactly midway between the lines numbered on the diagram are always put into the class which lies next to the right of the point of crossing; in other words, in the direction toward which the hands of a clock move. Thus a reading falling midway between 5 (50°) and 4 (40°) on the *Lg* side of the vertical would be put into class *Lg* 4; if it fell in a corresponding position on the *Sm* side of the vertical, it would be included in class *Sm* 5. When to the readings for an animal headed away from the observer are added those for the same animal headed in the opposite direction, — the latter would lie in the lower half of the circle, — the possible error resulting from this method of recording is counterbalanced and the effect thus eliminated.

From what has been said it can be seen at a glance that the five readings shown in the illustrative figure (Figure 5) fell into the following classes: one in class 0; one in class *Sm* 1; one in class *Sm* 3; and two in class *Sm* 5.

Something must be said with regard to the disposition to be made of those cases in which the worm turned more than 90° , and so crossed the circle at some point in the dark half of the field. There are three possible ways in which these cases might be treated. Either (1) ig-

nore the response, (2) recognize as many classes in the dark field as in the light one, or (3) regard the response as equivalent to that of an animal crossing the circle in the light field at an equal distance from the directive axis. To ignore the response would obviously give unsatisfactory results, for such animals certainly exhibit strong responses either toward or from a given light. To create of them separate classes would also be undesirable, for the records should express the degree to which the worm turned from the normal, or, putting it the other way about, how closely it came into orientation in line with the axis of the lights. Since 90° (class 9) represents the extreme possibility of turning from the normal axis, the creation of further classes for crossings in the dark field would be misleading. The third possibility is obviously the one to be adopted. Thus, if an animal turned so far as to pass over the line at the point 13 on the side toward the small light, the trial was recorded in class *Sm* 5.

After the foregoing explanation the accompanying table (Table I) will be easily understood. This gives the results of 100 trials made with 10 individuals exposed to unilateral illumination, in this case to the large light. The 19 vertical columns, numbered each way beginning with 0 and going to 9, correspond to the classes described above. The individual numbered 3 (marked with an asterisk) is the same one that is represented in Figure 5. In the columns next beyond columns 9 are recorded the total number of crossings made on the *Lg* side of the 0 class and on the *Sm* side of that class, while in the columns next beyond these are indicated the number by which one of these exceeds the other. From this it can be seen at a glance that when the worms were headed away from the observer (left side to light), they crawled only 4 times toward the light (+ responses), 38 times away from the light (— responses), and 8 times straight ahead (indifferent responses). Thus there is an excess of 34 trials on the side of *Sm*. The records for the worms headed in the opposite direction (right side to light) are not so striking. These are: toward *Lg*, 17; toward *Sm*, 26; indifferent, 7, giving an excess of only 9 toward *Sm*. Adding these two sets together, we have: *Lg* (+), 21; *Sm* (—), 64; 0 (\pm), 15; excess in favor of *Sm*, 43. Since 100 trials were made altogether, 43 per cent may be taken as an index of the negative response of *Allolobophora foetida* to the large light alone under the conditions of the experiments.

The results of 100 trials under each of the three conditions, large light only, small light only, and both lights simultaneously, are summarized in Table II. The general arrangement of the data is similar to that in Table I, except that the details of individual reactions

TABLE I.
REACTIONS OF *Earthworm* TO LARGE LIGHT. (*Experiments B and C combined.*)

	No. of the Individual.	Excess to lg.	Total to lg.	9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9	Total to Sm.	Excess to Sm.
Headed away from observer (left side to light).	1	5	..
	2	4	..
	3	4	..
	4	4	..
	5	3	..
	6	4	..
	7	3	..
	8	3	..
	9	3	..
	10	5	..
Total	4	8	4	10	6	5	7	3	3	38	34
Headed toward observer (right side to light).	1	..	1	1	..	3	..	1	1	..
	2	3
	3
	4
	5
	6
	7
	8
	9
	10
Total	17	7	6	6	6	5	1	2	26	9
Total, both positions	21	15	10	16	12	10	8	5	3	64	43

have been omitted. For the sake of brevity the worms are spoken of as "headed north" or "headed south," in place of "headed away from observer," and "headed toward observer," respectively.

The first of these sets of records — that resulting from the use of the large light alone — has

just been discussed in commenting on Table I. The per cent of negative reactions to the *small* light alone is even larger than that to the large light alone. It will be noted that the worms turned 68 times to *Lg* (—) and only 12 times to *Sm* (+), making an excess of 56 times, or 56 per cent, away from the light. In the case of *both* lights, however, the records in the two directions nearly balance. They read: to *Lg*, 40; to *Sm* 41; indifferent 19. This leaves an excess of only one record, or 1 per cent of the whole, in favor of the side toward the small light.

By regarding merely the total number of crossings at one side or the other of the normal, no account is taken of the degree of divergence from that line. This, however, is shown within limits of 10° by the segregation of the records into classes, as shown in the

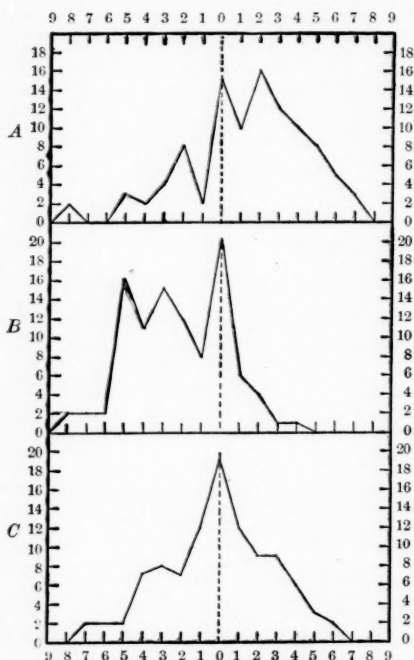


FIGURE 6. Frequency polygon showing the distribution of reactions of the earthworm to (A) the large light alone, (B) the small light alone, and (C) both lights used simultaneously (100 trials under each condition).

tables; but it may be more quickly perceived by the use of a graphic method — by plotting the records in the form of frequency polygons, as seen in Figure 6. Along the abscissae are laid off 19 divisions, corresponding to the 19 classes, as in the tables. Here, too, the relative positions of the lights are always the same — the large light at the

TABLE II.

REACTIONS OF *Earthworm* TO LARGE LIGHT ALONE, TO SMALL LIGHT ALONE, AND TO BOTH LIGHTS SIMULTANEOUSLY.
(Experiments B and C combined.)

Lights used.	Direction headed.	Excess to <i>Lg.</i>	Total to <i>Lg.</i>	CLASSES.																		Total to <i>Sm.</i>	Excess to <i>Sm.</i>	
				9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8			9
Large	No.	..	4	..	1	1	1	1	..	8	4	10	6	5	7	3	3	38	34
	So.	..	17	..	1	3	1	3	7	2	7	6	6	6	5	1	2	26	9
Total	.	..	21	..	2	3	2	4	8	2	15	10	16	12	10	8	5	3	64	43
Small	No.	28	34	..	2	1	1	7	5	9	6	3	10	3	1	1	1	6	..
	So.	28	34	1	1	9	6	6	6	5	10	3	3	6	..
Total	..	56	68	..	2	2	2	16	11	15	12	8	20	6	4	1	1	12	..
Both	No.	6	23	2	1	1	4	4	4	7	10	7	2	3	2	2	1	17	..
	So.	..	17	1	1	3	4	3	5	9	5	7	6	4	1	1	24	7
Total	40	2	2	2	7	8	7	12	19	12	9	9	6	3	2	41	1

left, the small at the right. The number of responses falling in each class are recorded on the corresponding ordinates. In the first polygon (Figure 6, *A*) are represented the experiments with the large light alone (as recorded in Table II), where, it will be noticed, the polygon lies mainly on the side away from the light; similarly the second polygon (Figure 6, *B*) lies chiefly on the side away from the small light, which was alone used in this case. The third figure (Figure 6, *C*) represents the data when both lights were used, and is remarkably symmetrical, with its mode at 0. This indicates a condition as nearly balanced as could well be expected.

These results on the earthworm would appear to admit of only one interpretation, namely, that the *intensity* of the light is the controlling factor in its reactions and not the size of the field from which the light is derived. The latter, in fact, appears to have no influence whatever. This is in exact accordance with what would be expected in the case of an eyeless animal. It possesses no organs so differentiated as to be able to discriminate space relations in objects beyond its touch; there is no mechanism for preserving these relations in space, as the light from the different parts of the object falls upon the sensitive portion of the animal, and consequently there is no suggestion of image formation. The light stimulates according to its intensity only, and since the intensity is the same on each side, the animal responds by approximately an equal number of deviations in each direction.⁶ It may be asked why, if the amount of stimulation on the two sides is balanced, the worm does not always crawl in a straight line, deviating neither one way nor the other, and always cross the circle so as to fall in the 0 class. This is probably for the same reasons that with unilateral illumination the worms do not uniformly turn away from the light. Similarly Parker and Arkin (:01) pointed out that in their experiments only 30.2 per cent of the "head movements" were away from the light, 65.6 per cent being straight ahead and 4.2 per cent toward the light. These authors attributed the movements toward the light to the uneven surface of the paper on which the worms were allowed to crawl, and to other disturbing influences. In view of Harper's recent work (:05), it would seem that conditions of uneven or one-sided expansion or contraction of the animal might have some influence in producing these

⁶ Loeb (:05, p. 2, footnote) maintains that "if two sources of light of equal intensity and distance act simultaneously upon a heliotropic animal, the animal puts its median plane at right angles to the line connecting the two sources of light." This statement needs a number of qualifications.

results, by exposing the deep-lying cells — which are supposed to be the organs stimulated — unequally to the light. Undoubtedly, too, these animals are not the simple mechanisms that we are often inclined to consider them, but are subject to certain internal conditions — physiological states, if we care to call them so — which are beyond our observation and control, and by their changes produce corresponding irregularities in the results. On this account it is important to use animals for experimentation that have previously been subjected for a considerable period to constant conditions.

2. *Land Planarian (Bipalium kewense Moseley).*

The so-called eyes of planarians are remarkably uniform throughout the group in general plan of construction. Each consists of one to several sense elements, or cells, backed by a pigmented cup, which is in turn composed of one or a few cells. These eyes have no apparatus for the formation of an image, but are constructed in such a way that generally light from only one direction can affect a single eye at a given time. For this reason they are often spoken of as *direction eyes*. In the genera *Planaria*, *Dendrocoelum*, and related forms, only two eyes are present; but in others, such as *Polycelis* and the land planarians, eyes may be present in great numbers.

Bipalium is a well-known genus, comprising a large number of species, mostly indigenous to Japan, China, India, Ceylon, and the Malay Archipelago. There is well established in certain greenhouses in Cambridge a species, the original home of which is unknown. This species was first described by Moseley ('78) from a specimen obtained in the Kew Gardens, England, and was named by him *Bipalium kewense*. Since that time it has been found in hothouses in widely separated localities in nearly all parts of the globe, and it is generally believed to have been unintentionally distributed with consignments of plants, either from its original home or from other places where it had become established. Woodworth ('96) reported it from Cambridge, Mass., in 1896. A form described from Landsdowne, Pa., by Sharp ('91) as *Bipalium manubriatum* is probably the same species; and Woodworth ('98) has since reported it from other localities in the United States (Baltimore, Md., Pittsburg and Allegheny, Pa., and Springfield, Ohio).

Bipalium kewense is the largest of the land planarians, the specimens ordinarily ranging from 12 cm. or 13 cm. to 25 cm. in length; and Woodworth ('96) records one 30 cm. long. These measurements are those of the worm in the extended condition, which is assumed in

crawling. The body is capable of great contraction, so that a worm which is, when crawling, 25 cm. long, may contract to a length of only 5 or 6 cm. (see figures given by Bell, '86, pl. 18). The head when extended is semilunar, or shaped like a battle-axe (see Figure 9, p. 364), and is about twice as broad as the body immediately behind it. The eyes have been described in other species of *Bipalium* by Moseley ('74, p. 144) and in *B. kewense* by Bergendal ('87) and Jänichen ('96, p. 275; Taf. 10, Figur 18; Taf. 11, Figur 21). Bergendal ('87, p. 49) describes the position and arrangement of the eyes as follows: "Eyes occur in this species in enormous numbers. They form a zone of three or four rows near the margin of the head, and are also placed on the sides (not on the back) of the whole body, even to the hindmost end." The largest eyes are on the head and immediately behind it, and they are closer together in those regions than on the body farther back. According to Jänichen ('96, p. 276), each pigment cup has the form of a hollow hemisphere, the convex side of which is turned inward, while the flat side, which is open, is directed outward. The pigment spot, which forms the background of the sensory cells, is composed of a single cell. From three to six flattened sense cells lie in the pigment cup, and, as in *Polycelis*, the eyes farther posteriorly are not only smaller, but usually have a smaller number of sense cells.

Hesse ('97) has discussed from a theoretical standpoint the manner in which the eyes of planarians probably function. He deals in this case with those forms which possess only two eyes. The diagrams which he gives ('97, p. 575) are reproduced in Figure 7, and require only a brief explanation. When there is only a single sense cell in the pigment cup, it may be stimulated by light coming from various angles, covering a considerable range, that is, by any light which is able to enter the cup. Thus the effect would be the same in the left of the two eyes represented in the diagram for light coming in any of the directions shown by the arrows in *A*, *B*, *C*, or *D*. If, however, there were a number of sense cells in the cup, only a part of these would be reached by the light coming from any one of the directions shown, and the light would strike different cells according to the direction from which it came. In the first case, the structure of the eye would not furnish any opportunity for determining the direction of the light within the range of the arrows in *A* to *D*; in the second case it would, since under the conditions shown in *A* the cells on one side of the cup (posterior) would receive the light, whereas in *D* those of the other side would receive it. This condition may be considered as the beginning of a crude image-forming apparatus, the eye approximating in a rough way the concave mosaic type. These are theoretical deduc-

tions from the anatomical conditions; no test has been made to show whether the physiological action supports the hypothesis. The eyes of *Bipalium* are so small, and their axes so variously directed, that it seems doubtful if the individual eyes can have more than a very general directive function in the reception of light. Although in general they open directly outward, — as mentioned by Jänichen ('96), and as may be seen in the photograph of a portion of the border of the head

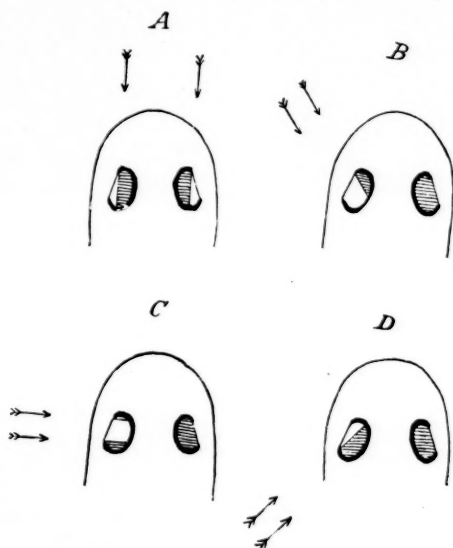


FIGURE 7. Various illuminations of the *planarian* eye with light coming from different directions. The optic cups are drawn too large in proportion to the size of the head. The arrows indicate the direction of the light; the portions of the interior of the cup not reached by the light are shaded. — From Hesse, '97.

reproduced in Figure 8, — they are nevertheless not all accurately oriented in that way; furthermore, the position and direction of each eye naturally varies with the movements and contractions of the animal. In general, however, they do open outward, as is represented diagrammatically in Figure 9. It will be noticed that the eyes of any particular region are so arranged that they usually receive light exclusively from a direction normal to that part of the surface of the head beneath which they lie, as indicated by the arrows. The efficiency of

this arrangement is greatly increased by the lateral extension of the



FIGURE 8. Photomicrograph of a portion of the margin of the head of *Bipalium*, showing the position and arrangement of the eyes. $\times 70$.

head, which allows room for a greatly increased number of eyes in its anterior border. Taken as a whole, this arrangement might be roughly

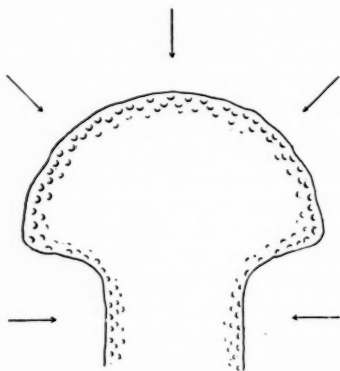
compared to a single convex mosaic eye, such as is found, for example, in the Entomostraca.

Below are described the results of physiological tests with lights of different sizes, in an attempt to determine in how far the eyes may act in this way.

It is a well-known fact that most planarians avoid the light (the exceptions being certain chlorophyll-bearing forms), and they have long been used for work in phototropism. *Bipalium* appears never to have been used for experimental purposes, although the fact that the land planarians share with the water inhabiting forms aversion to light was remarked upon more

FIGURE 9. Diagram of the head of *Bipalium*, to show how light coming from different directions (indicated by the arrows) may affect only certain of the eyes.

than sixty years ago by Darwin ('44). That they are also nocturnal in their habits has been commented upon by various authors since that



time. Bell ('86, p. 168) remarks that "There can be no doubt as to the sensitiveness of *Bipalium* to light," but he referred only to what he supposed was the effect of strong light in causing the worm to break up into a number of pieces, and not to the directive action of the light. As a matter of fact, *Bipalium kewense* is exceedingly sensitive to light, of even a very low intensity, falling upon it from the side, and responds immediately by turning away from the light. For this reason, and because it is easy to keep and to handle, it is an excellent animal for experimental purposes. Like most planarians, it creeps with an even, gliding motion, the head being slightly raised and waved to right and left, apparently in searching movements, as the worm crawls forward. In the daytime this *Bipalium* is usually to be found coiled up underneath flower pots which sit on the ground in warm, moist rooms of greenhouses; and it is probable that it comes out and moves around only at night. What it eats appears not to be known with certainty, but the common opinion seems to be that, like other turbellarians, it is carnivorous. Some of the related forms are known to eat earthworms, and certain authors believe the same to be true of *Bipalium kewense*.

Description of Experiments. The experiments on *Bipalium* were conducted in the same manner as those on the earthworm, except that the ground glass on which the animals were placed was supported about 1 cm. above the table by means of small wooden blocks, or feet, glued to the under surface of the glass at its four corners, instead of being swung free by strings from the ceiling. By lifting the plate very slightly, it could be turned easily in any direction. This had the advantage that when the worm was once in the proper position, the wooden feet could be brought in contact with the table again, the plate thus remaining perfectly steady and horizontal. When the worm was creeping well in the shaded area, the plate was moved so that about 5 mm. of the anterior end of the worm was brought out, in the normal position, into the influence of the light, and the record was taken when the animal's head reached the *first* circle, instead of the third, as in the case of the earthworm. It thus crawled a distance of only 4.5 cm. at each trial; but the reactions of *Bipalium* are usually so immediate and definite that this distance seemed sufficient for the purpose of the experiment.

The results of 10 trials each, with 10 worms (100 trials in all), when both lights were operative, are shown in Table III. It will be noticed that more than half of the 100 trials fall in the 0 class, and that only a single record falls more than two classes to right or left of that position. This means that in only one instance did a worm deviate more than 25° from the normal axis, thus showing a remarkably well bal-

lanced condition of all stimuli. The excess of responses towards *Sm* over those towards *Lg* is, however, comparatively large, being 17 per cent. The real nature of the results, with the conspicuous "mode" at 0, may be more readily appreciated when the data are plotted in a frequency polygon, as has been done in Figure 10. These results indicate that *Bipalium* has, to a slight extent, the ability to appreciate differences in area, since it responds by turning away from the larger luminous area more often than from the smaller. It is possible that a considerably larger area, even though the total amount of light were no greater, might have a more decided effect. If the arrangement of the eyes around the circumference of the head acts, as has been suggested, in a manner similar to a single so-called mosaic eye, forming roughly what Exner terms an apposition image, it can be seen that

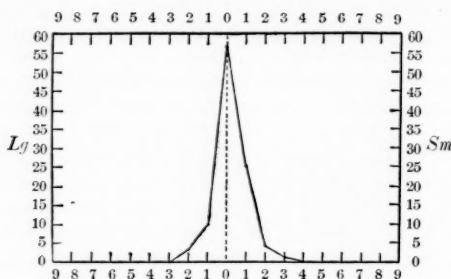


FIGURE 10. Frequency polygon constructed from the results with *Bipalium* shown in Table III (100 trials to both lights used simultaneously).

light must come from rather widely different directions in order to enter an appreciably larger number of the cups than would be affected by light from a single point. This is owing to the comparatively large semicircle of the head and the irregularity in arrangement of the pigmented cups, as well as to their shallowness and their great distance apart, as compared with the ommatidia of, e. g., an insect's eye. It is not surprising, then, that light from the different parts of a field only 41 cm. across and 2 meters away (the most extreme rays making with each other an angle of only about 12°) produces little noticeable effect in the reactions of such a worm.

After the above set of experiments had been made it was found that a disturbing factor had influenced some of the work with *Bipalium*. This factor was a light draught of air sweeping the table

TABLE III.
REACTIONS OF *Bipalium kewense* TO BOTH LIGHTS.

Lights used.	Direction headed.	Excess to <i>Lg.</i>	Total to <i>Lg.</i>	CLASSES.																			Total to <i>Sm.</i>	Excess to <i>Sm.</i>
				9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9		
Both	No.	...	9	3	6	28	11	1	1	13	4	
	So.	...	4	4	29	14	3	17	13	
Total	13	3	10	57	25	4	1	30	17	

from left to right; it came from a ventilator in the south wall of the room, which was sometimes open, sometimes closed. No record was made as to whether it was open or closed when the above experiments were made; but in the light of subsequent experiments made to test the effects of the draught the records themselves seem to show that it must have been closed. This appears from the fact that, in the experiments made to test the effect of this current of air, it was found that the worms were very sensitive to it, and that in all cases when the ventilator was open the "mode" for the reaction was pushed over to the right of the 0 class, the light being in these tests purposely non-directive, as it came from a lamp directly above the normal axis of the circle.

3. Mealworm (*Larva of Tenebrio molitor* Linn.).

The negative phototropism of the mealworm has been commented upon by Loeb ('90, pp. 84, 85), who found that these animals not only moved away from the side of a dish from which the light came but that they remained in the darkened half of the dish when the plane between the dark and the light portions coincided with the direction of the rays. A few responses to a single light as used in these experiments confirmed Loeb's conclusions that the animals are markedly negative in

their reactions to light; consequently a large series of experiments was made to determine their reactions to the two lights of different area.

The larvae were placed, one at a time, upon the ground-glass plate used in the previous experiments, which, as in the case of *Bipalium*, was supported about 1 cm. above the table by means of small wooden feet. As with *Bipalium*, too, the records were taken when the larva reached the first, or inner, circle, so that it crawled a distance of only about 5 cm. In the earlier experiments the glass plate was kept moist in the belief that the moisture caused the larva to keep up its crawling motion; but later the plate was used dry without essential difference in the results. The animals usually started promptly and crawled rather rapidly and uniformly, as soon as placed on the plate, but in some instances they showed considerable hesitancy and made trials in various directions before going ahead.

They appear to have three characteristic modes of progression: (1) The most usual manner is by means of the legs alone, the posterior portion of the body being dragged along passively. This part may be held straight, but sometimes it is slightly curved to one side, in which case it is possible that its position influences to some extent the direction in which the animal turns. (2) The larva occasionally crawls by alternate elongation and contraction of the body (made possible by the telescoping movements of the segments), much as an earthworm crawls, and at such times the anterior end is often raised into the air and waved about more or less. (3) The larva may also move backward for a short distance at about the same rate that it normally crawls forward. It seldom goes backward more than two or three centimeters, and then starts forward again, apparently *always turning in one direction or the other*, and not going forward in the same line in which it was moving backward. This last reminds one somewhat of the motor reaction described for Protozoa and some other animals by Jennings; but whether it is used for the same purpose in response to strong stimulation or other conditions does not concern us here, since it is not the usual method of orientation to light of moderate intensity.

In the experiments with light falling upon one side only, the larvae were given five trials headed in one direction, and then five headed in the opposite direction; but in the trials with both lights at once they were headed alternately in the two directions, — one trial in one direction and the next in the opposite. Since in both cases there are the same number of trials in each direction, it is not probable that this difference of method affects the results. Only 50 trials each were made with the two lights separately, whereas 200 trials were made with both operating at the same time. The same five individuals were

employed in the trials with the lights used separately and in 100 of the 200 trials with both lights together; in the remaining trials with both lights five other larvae were employed. The results of the experiments on the larvae of *Tenebrio molitor* are classified and summarized in Table IV.

The preponderance of reactions away from the light is strikingly shown in the first two sets of experiments, where unilateral illumination was tested. With the large light there was not a single positive reaction, and only 4 out of 50 fell in the 0 class, so that 46, or 92 per cent, of the reactions can be counted as distinctly negative responses. The records with the small light alone are somewhat more scattering, but are nevertheless preponderatingly negative. Only 8 records are towards the light, while in 41 out of the 50 trials the animals turned towards the dark, giving an excess of 33, or 66 per cent, in that direction. The responses when the two lights act simultaneously are almost equally balanced as between the two sides, by far the

larger number of records on each side falling near the 0 class, which itself contains 43 of the 200 records, or nearly one fourth of the whole number. This result may be much more quickly and completely grasped from an inspection of Figure 11, C. On the side towards the

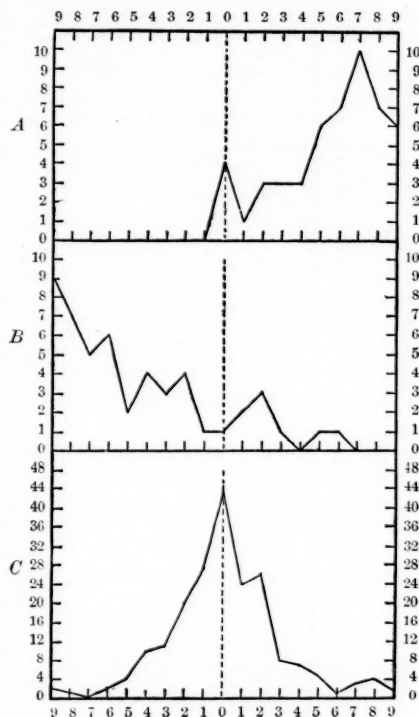


FIGURE 11. Frequency polygon constructed from results with the mealworm shown in Table IV. A, 50 trials to large light alone; B, 50 trials to small light alone; C, 200 trials to both lights used simultaneously.

large light are 77 records; on that towards the small light 80, giving an excess of only 3 records in the direction of the small light, which is only 1.5 per cent of the total number of trials.

Polygons *A* and *B* are plotted from the data of the experiments with one-sided illumination, when the large (*A*) and small (*B*) lights were used separately.

The conclusions to be drawn from the reactions of the larvae of *Tenebrio molitor* are, it would seem, as follows. These animals are almost uniformly negative to unilateral illumination in light of moderate intensity. The ability of the eyes to form distinctive images of objects differing considerably in size is wholly lacking, or at least practically so, as is to be inferred from the reactions of the animals when exposed to the simultaneous influence of the two light areas used in these experiments. It is perhaps worth noting that the excess of 1.5 per cent is away from the large light, and that in no case did the larvae turn towards the large light when that light was used alone, whereas a few did turn towards the small light when that was the only one used. Still, it would not be very surprising if in a repetition of this series of experiments the balance should lie on the opposite side of the zero class. The magnitude of this difference is probably too small to be of significance.

The above results are what would be expected in view of the rudimentary condition of the eyes in the mealworm. The eyes apparently consist of only two or three ocelli on each side of the head, arranged in a vertical row immediately behind the base of the antennae. Examination of the chitin immediately overlying them, even after it had been boiled in caustic potash, has shown no thickenings or differentiations that might serve as lenses. The eyes are so small that they can scarcely be seen without the aid of a lens.

Loeb ('90) has remarked on the relation existing between the reactions of these animals to light and moisture and their natural habits.

4. Sow Bug (*Oniscus asellus* Linn.).

This widely distributed, active little isopod may be found in abundance beneath stones, bark, pieces of wood, etc., in the woods in the vicinity of Cambridge. Its retiring habits, indicating an avoidance of light, and the ease with which it can be kept and handled in the laboratory, suggested that it might be a suitable form for use in these experiments. Handling often has at first an inhibitory effect as regards locomotion, but this is usually overcome in a short time, and the animals then normally start off as soon as released. The eyes are

small, but still readily visible, each consisting of a group of about 20 ocelli situated on the side of the head at the base of the antero-lateral lobe.

The animals were oriented in the proper position by placing them within a small rectangular glass frame without top, the glass being

covered with black paper to exclude the light until the pen thus made was lifted up. The frame was oblong, and just large enough to enclose the *Oniscus* easily without allowing it to turn around. With a little care the frame could be readily moved on the table (the glass plate was not used) to the position desired, and with the animal headed in either direction. When it was lifted off, the animal was left exposed to the lateral influence of one or the other or both of the lights, as the case might be, but free to move in any direction. The records indicate the place where it crossed the second of the three circles inscribed on the table, — the one with a radius of ten centimeters. As the animals usually took a straight, or only slightly curved course, this was

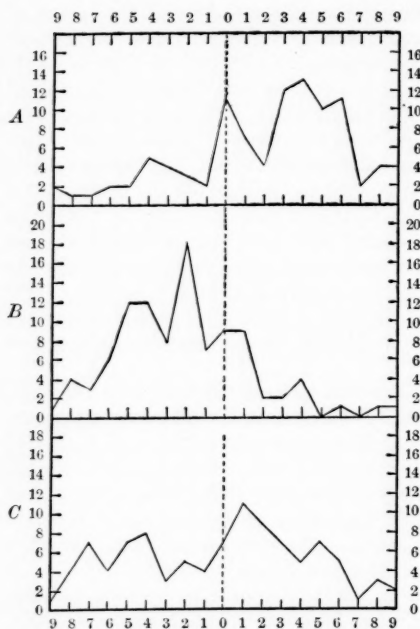


FIGURE 12. Frequency polygon constructed from results with *Oniscus* shown in Table V. A, reactions to large light alone; B, to small light alone; C, to both lights used simultaneously (100 trials under each condition).

practically the distance travelled by them in each of the trials.

The experiments with the lights used singly showed *Oniscus* to be decidedly negative in the character of its reaction, but by no means so strikingly so as the *Tenebrio* larva. In *Oniscus*, as may be seen from an inspection of Table V, only 45 per cent to 51 per cent of the reac-

TABLE V.
REACTIONS OF *Oniscus asellus* TO LARGE LIGHT, TO SMALL LIGHT, AND TO BOTH LIGHTS.

Lighth used.	Direction headed.	Per cent of Excess to Lg.	Excess to Lg.	Total to Lg.	CLASSES.																			Total to Sm.	Excess to Sm.	Per cent of Excess to Sm.
					9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9			
Large	No.	9	1	1	3	2	1	1	4	2	2	7	6	7	8	2	1	2	37	28	56
	So.	13	1	1	1	2	1	2	2	2	1	7	5	2	5	7	3	3	..	3	2	30	17	34
Total	22	2	1	1	2	2	5	4	3	2	11	7	4	12	13	10	11	2	4	4	67	45	45
	No	50	25	35	..	1	1	2	7	7	4	8	5	5	7	..	2	1	10
Small	So.	52	26	36	1	3	2	4	5	5	4	10	2	4	2	2	..	3	..	1	..	1	1	10
	Total	51	71	1	4	3	6	12	12	8	18	7	9	9	2	2	4	..	1	..	1	1	20
Both	No.	15	1	2	3	1	2	2	1	2	1	4	7	7	1	5	3	5	..	1	2	31	16	32
	So.	18	9	28	..	2	4	3	5	6	2	3	3	3	4	2	6	..	4	..	1	2	..	19
Total	43	1	4	7	4	7	8	3	5	4	7	11	9	7	5	7	5	1	3	2	50	7	7

tions were away from the light in excess of those toward the light, whereas in *Tenebrio* the excess in this direction ranged from 66 per cent to 92 per cent of the total number of trials. The results of the experiments on *Oniscus* are represented graphically in Figure 12.

In the trials with both lights the records on the two sides are nearly balanced, there being an excess of only 7 per cent of the reactions away from the larger light. This excess again lies in the direction we should expect if the eyes enable the animal to discriminate between the two luminous areas, but, as in the case of *Tenebrio*, it is too small to be of great significance. It will be noticed by comparing the figures obtained with the large and small lights used separately that the result is the opposite of that obtained with the two lights acting simultaneously, and also opposite to the results in the case of *Tenebrio*, for in *Oniscus* a larger percentage turned away from the small light than from the large one. Since the experiments on *Tenebrio* and on *Oniscus* were performed at different times, it is possible that a difference in the (absolute, not relative) intensities of the lights at the two times may be responsible for the want of harmony in the results. When both lights were used at the same time, they were adjusted so that their intensities were equal, and therefore no errors could have arisen from this source.

It may be concluded from these experiments that, although *Oniscus* has apparently much better developed eyes than the larva of *Tenebrio*, its responses to light are of a considerably less definite character. This means that with unilateral illumination *Tenebrio* turns toward the light much oftener than *Oniscus*, and although in a frequency polygon representing the reactions to light the mode for each of the animals falls upon the side away from the light, in the case of *Oniscus* it falls much nearer to the median (indifferent) line than it does in *Tenebrio*. This may be seen by a comparison of Figures 11 and 12. The greater delicacy of the adjustment to light conditions in *Tenebrio* is also shown in the reactions to the two lights used simultaneously. There the responses of this animal are concentrated about the indifferent or zero class (Figure 11, *C*), whereas in *Oniscus* under similar conditions (Figure 12, *C*) they are scattered much more evenly through the nineteen classes. This should not be taken to mean that *Tenebrio* probably has better vision than *Oniscus*, but merely that in nature its phototropism is more strongly negative, a state which may be independent of the acuteness of vision, but is commonly related to the conditions of existence. Whatever evidence is afforded by these experiments as to the comparative ability of the eyes of *Tenebrio* larvae and of *Oniscus* to form images lies in the fact of the apparently

greater efficiency of the eyes of the latter animal in distinguishing between a large and a small area — an efficiency which is indicated in one case by 7 per cent, in the other by 1.5 per cent. If *Oniscus* were naturally as sensitive in its responses to light as *Tenebrio*, this difference would probably be greater. In other words, the image-forming power of the eye of *Oniscus* probably exceeds that of *Tenebrio* more than appears in this method of experimentation, owing to the fact that even to unilateral illumination the responses of the former are so much less definite than those of the latter.

5. *Cockroach* (*Periplaneta americana* Linn.).

This cockroach, which abounds in slaughter-houses and other similar situations where there is much waste matter that can serve as food, possesses large compound eyes with a great number of ommatidia. Latter (: 04, p. 88), in speaking of the related species, *P. orientalis*, says: "To what extent the compound eyes are capable of forming a distinct image of surrounding objects we cannot say, but it is evident that they are keenly sensitive to differences of light and shade from the speed with which a cockroach makes for dark corners and crevices when disturbed." This characteristic of cockroaches is very evident to any one who has ever observed them. If a number of them are in a glass jar, the cover may be removed with comparatively little danger that any of them will escape so long as the mouth of the jar is turned toward the light; but if its position is reversed, they will usually escape from it very quickly. These and similar observations led to the selection of this animal also for experimentation with the lights of different area.

Cockroaches are so active and comparatively difficult to handle that it took considerable experimenting to devise a scheme for getting them oriented in the proper position without the introduction of disturbing factors. If one attempts to liberate them from the hand, their struggles usually result in their being in an undesirable position when released, instead of exactly in the normal position. Finally, after employing several unsuccessful devices, the following was made use of. A glass cylinder some 15 centimeters in diameter and 20 centimeters high was placed endwise on the table and so arranged that from one side of the bottom a low, narrow glass runway led off for a distance of about 5 centimeters. This runway was large enough to allow a cockroach to pass through it easily, but not large enough to permit the insect to turn about. It was covered with black opaque paper, which cut off the light and made its interior dark. This

apparatus could be placed with the axis of the runway directly over the normal axis of the diagram on the table and so oriented that its anterior end was directed either north or south at will and coincided with the directive axis. The animal to be tested was then dropped into the cylinder and made to move about until at length it entered the runway. When it came out at the other end of the runway, it was properly oriented, with one light at its right, the other at its left. Some of the most active individuals would run through this passage and emerge without stopping; but there was much individual variation in their behavior in this respect. By far the larger number of them stopped in the runway as soon as their antennae projected from the farther end, and there they would remain, waving the antennae about or cleaning them by drawing them through their jaws, but refusing to go farther without being stimulated from the rear. Such individuals were stimulated by pushing a small block of wood into the runway behind them until it came against the cerci or the hind legs. The block was made nearly as broad as the runway in order that it might strike the animal evenly and not stimulate one side more than the other. Usually the slightest touch was sufficient to start the insect from the runway, but some individuals seemed very reluctant to leave, and in a few instances, immediately they were outside, they turned about and regained the shelter they had just left. Most of them, however, as soon as outside, ran ahead steadily and rapidly, either going nearly straight or swerving to one side or the other; others would hesitate or even stop altogether, and then make sharp turns, often going off finally in a direction entirely different from that which they first took when they came out of the runway. The records indicate the points at which they crossed the outer circle — the one having a radius of 15 centimeters.

Table VI summarizes the results of 98 trials with the large light alone and 200 each with the small light alone and with the two lights used simultaneously. As in the preceding experiments, Figure 13 shows the records in graphic form.

These records show that *Periplaneta* is decidedly negative to light from one side, — 42.8 per cent of the reactions may be so regarded in the case of the large light and 55 per cent in that of the small light. Here the peculiarity will be noticed that, as in the case of *Oniscus*, there was a larger per cent of reactions away from the small light than away from the large one. Moreover, in the cockroach, as may be seen from the lower third of Table VI and from Figure 13, *C*, there were more turnings from the small light than from the large one, when both were used. This excess is very small, it is true, — only 9 reactions in

TABLE VI.
[REACTIONS OF THE *Cockroach* TO LARGE LIGHT, TO SMALL LIGHT, AND TO BOTH LIGHTS.

Ligite used.	Direction headed.	Per cent of Excess to Lg.	Excess to Lg.	Total to Lg.	CLASSES.																			Total to Sm.	Excess to Sm.	Per cent of Excess to Sm.
					9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9			
Large	No.	12	2	..	1	3	..	1	5	3	2	9	8	1	4	4	2	1	3	34	22	44.8
	So.	12	2	3	2	2	..	1	2	5	5	9	10	4	2	1	..	1	..	32	20	40.8
Total	24	4	3	3	5	..	2	7	8	7	18	18	5	6	5	2	2	3	66	42	42.8
Small	No.	47	47	66	..	1	1	1	4	14	16	15	15	5	2	2	2	6	2	19	
	So.	63	63	77	4	3	2	5	7	19	16	16	5	9	3	4	2	3	2	..	14	
Total	55	110	143	4	4	3	6	11	33	30	32	20	24	8	6	4	5	6	..	2	..	33	
Both	No.	33	1	2	1	1	1	4	2	6	15	27	23	8	6	1	2	..	40	7	7	
	So.	16	16	40	2	..	1	8	3	12	14	36	11	8	2	3	24	
Total	4.5	9	73	1	2	3	1	2	12	5	18	29	63	34	16	8	4	2	..	64	

200, or 4.5 per cent, — but it is difficult to explain why they are in the direction of the larger light, instead of the reverse. In the first set of 100 trials with both lights the records of particular individuals

were not kept separate, and as it was thought that possibly some abnormal animal had influenced the total, the whole series was repeated on another set of five individuals, these matters being kept in mind; but the results were entirely comparable with those obtained in the first set of experiments. Such being the case, the two sets of records were combined, and are so represented in the table and the diagram.

The only plausible explanation of this unexpected result which offers itself at the present time is, that at least a portion of the animals were influenced by other factors as well as by the light from the two primary sources. Cockroaches, if undisturbed, are apt to make themselves at home wherever they are put, and usually soon settle down to cleaning their antennae or to making an inspection of their surroundings, apparently irrespective of

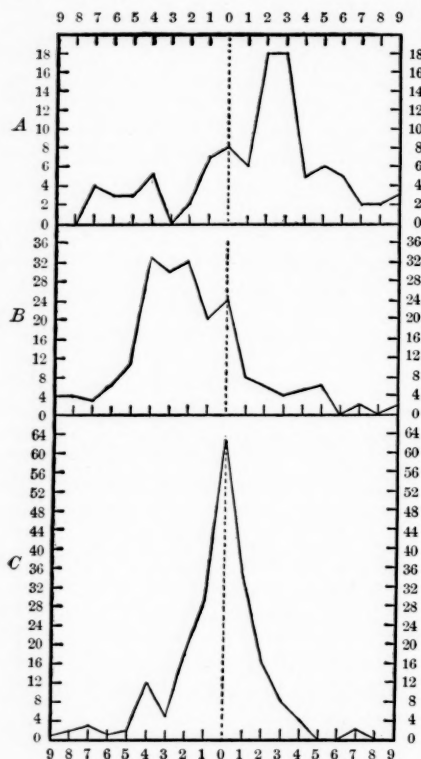


FIGURE 13. Frequency polygon constructed from results with *cockroach* shown in Table VI. A, 98 trials to large light alone; B, 200 trials to small light alone; C, 200 trials to both lights used simultaneously.

such influences as steady directive light. It has already been mentioned how the animals came to rest at waving the antennae about or cleaning

them. Similarly, they

would sometimes stop outside the runway and go through the same operations.

As a rule the animals which react most constantly and uniformly to directive light are those that are under more or less unnatural conditions, as was the case with the earthworm, *Bipalium*, *Tenebrio*, and, to a less extent, *Oniscus*, when placed on the glass plate or on the table top. These animals usually come to rest under normal surroundings only when a considerable portion of the body, especially the dorsal side, is in contact with something. Cockroaches, on the other hand, may often be found at rest upon the walls of the dimly lighted cellars and basements where they live. They do not by any means spend all their time in cracks and crevices, though they usually retire to such places when more strongly illuminated. In many animals the ordinary reactions appear to have an inhibitory effect on the reaction to light, so long as the animal is not disturbed in any unusual way. Or the animal may simply come to rest, and yet respond immediately to such constant stimuli as directive light or gravity if it be disturbed. Carpenter (:05) has pointed out, for example, that pomace flies (*Drosophila*) will come to rest in the darker portions of the dish with their heads turned away from the light, but if they be disturbed by turning the dish slightly, they respond at once with their ordinary phototropic reaction. Mechanical agitation has a similar accelerating effect upon their reaction to gravity. As will be described later, a frog may sit for a considerable time with the axis of the body at right angles to the direction of a light, which apparently has no effect upon him; but upon being stimulated in any non-directive way he will usually turn at once and face the light, or may even hop toward it. Similarly, reactions to food, to contact stimuli, etc., may inhibit entirely the ordinary reactions to light. Certain pycnogonids cease entirely their efforts to go toward the light when the feet can grasp the stems of hydroids, among which these animals normally live; while if they are placed in a dish of water where they are unable to grasp any such familiar objects, they are strongly phototropic (Cole, :01). In fact, Loeb ('90, p. 21, *et seq.*) made special mention of the inhibitory effect of contact stimuli in his pioneer work on phototropism.

Instances need not be multiplied. The point is that the cockroaches, not being under especially unusual conditions, may have been influenced by other stimuli or by physiological conditions which in the case of animals less "at home" would have been overcome by the phototropic response. This may account for the fact that the slight excess of reactions was in a direction opposite to what one would expect. But the surprising thing is that this excess should have been so small, for in an

animal with eyes comparatively so well developed we might expect more evidence of image-formation to be apparent in its reactions to the lights of different areas. An inspection of Figure 13, however, shows that the "mode" for the negative responses of the cockroach to unilateral light lies only 20° to 40° from the indifferent position, in which respect it agrees more closely with *Oniscus* (compare Figure 12) and differs markedly from the *Tenebrio* larva (Figure 11), although its eyes are undoubtedly vastly better adapted to ordinary vision than those of the mealworm. This means that the cockroach is less responsive to directive light than the mealworm, or at any rate that its responses are less definite and constant. Another factor which must be taken into consideration is the greater rapidity with which the former animal travels, so that in a given distance the light acts upon it during a much shorter interval than is the case with an animal which moves more slowly. Under these circumstances the records would tend to be less divergent; and undoubtedly this was an important factor in the reactions to both lights, where, it will be observed, the number of records in the 0 class was very large (Figure 13). The same factor would have a tendency to mask any differences there might be in the reactions to the two lights. This fault was partially corrected in the experiments by taking the records for the cockroach when it crossed the outer circle (15 cm. radius), whereas the records on *Tenebrio* were taken when it reached the innermost circle (5 cm. from the starting point).

The conclusions to be drawn from the experiments on the cockroach may, then, be stated briefly as follows: *Periplaneta americana* reacts negatively to directive light as used in these experiments in an excess of about 50 per cent (42 per cent to 55 per cent) of its responses. It possesses relatively large eyes, which, one would suppose from their structure, were capable of much better image-formation than those of any of the other forms so far employed; but the results of the experiments fail to confirm this point. The explanation is probably to be looked for in the fact that on account of the influence of other factors the reactions to light are masked, and probably to a certain extent inhibited.

6. Mourning-cloak Butterfly (*Vanessa antiopa* Linn.).

The work of Parker (:03) on *Vanessa* naturally suggested that animal as a favorable subject for these experiments. The following conclusions reached by Parker (:03, p. 467) are of importance in the present connection:

"3. *V. antiopa* creeps and flies toward a source of light, that is, it is positively phototropic in its locomotor responses.

"4. Its positive phototropism occurs with lights varying in intensity from 2 candle-power at 2 meters distance (0.5 candle-meter), to 250 candle-power at 2 meters distance (62.5 candle-meters). . . .

"10. *V. antiopa* does not discriminate between lights of greater or less intensity provided they are all of at least moderate intensity and of approximately equal size.

"11. *V. antiopa* does discriminate between light derived from a large luminous area and that from a small one, even when the light from these two sources is of equal intensity as it falls on the animal. These butterflies usually fly toward the larger areas of light."

It will be seen that Parker had already concluded what might be expected to result from experiments on these butterflies under the conditions of the present investigation. His conclusions were based in large part upon observations in the field, supplemented by a number of experiments conducted in the laboratory. These, while they seemed to establish the verity of his conclusions beyond a reasonable doubt, were largely qualitative in their character, and it seemed of interest to repeat them under conditions in which the intensities and comparative areas of the lights were accurately known. Specimens of *V. antiopa* were accordingly procured, and as it was desirable — considering the comparatively small space where the insects could be exposed equally to the two lights — to have them crawl instead of fly, the wings were clipped off a short distance from the body, leaving only short stumps, by means of which the animals could be easily handled. Two difficulties presented themselves. Many of the butterflies either made attempts to fly, which resulted in their flopping about helplessly on the table, or they feigned death when released and refused to move at all. It was found that by holding the animal by one wing-stump, it would usually struggle with its legs and the other wing-stump. If in such a state of activity it was placed on the table, it would seldom feign death, but would start at once to crawl off. Attempts to start the animals with exact orientation in the normal position were abandoned, since it was found that holding them by one wing was apt to impart a unilateral impetus to their first locomotor movements; furthermore, after starting to crawl they would often begin making attempts to fly, and so struggle about on their backs with their legs in the air, thus losing all orientation before they regained their feet and progressed again by creeping. For similar reasons no record was made of the angles at which the animals diverged from the normal; in fact, when they once began crawling well, they crawled, as a usual thing, directly toward the light. In some cases they would first crawl a short distance toward the small light and then turn and go toward

the larger light. Since such results appeared to be due to chance orientation at the beginning of the trial, or after the insect had lost its orientation by fluttering, the records of the direction of its response were not made until it had crossed a line, on either side, at a distance of about 25 cm. from the normal axis. In the later trials no attempt was made to place the insects in normal orientations at the beginning of the trials, but they were dropped at random as nearly as possible at the central position on the table. About the same proportion between negative and positive responses was obtained as when the attempt had been made to orient the animals.

In all 164 trials were made in this way upon 7 different individuals of *Vanessa*, with the following results:

Toward large light.	Indifferent.	Toward small light.	Total.
143	1	20	= 164

Thus it will be seen that 87.2 per cent of the responses were toward the large light; 12.2 per cent were toward the small light; while only a single one, or 0.6 per cent could be called indifferent. The excess of responses toward the large light over those toward the small was 123, or just 75 per cent of the whole. This result therefore confirms Parker's conclusion that *Vanessa antiopa* discriminates between lights of different area falling with equal intensity upon the animal. That so many as 12 per cent of the responses were toward the smaller light is probably to be accounted for largely upon the chance orientation and the condition of making the record as soon as the insect had crossed a given line at a certain distance from the starting place. One or two instances were observed in which the butterfly actually turned and went back toward the large light after having passed this limit in the direction of the smaller one.

7. *Water Scorpion* (*Ranatra fusca* Pal. B.).

The interesting work by Holmes (: 05*) on the reactions of the water bug *Ranatra* to light suggested this form as a favorable one for use in the study of image-formation. Except under certain conditions, *Ranatra* is very strongly positive to light, apparently of any intensity, and reacts to it with great uniformity and persistence. Holmes says (p. 315): "Light seems to dominate entirely this creature's behavior when the phototactic reactions are once started. It does not manifest any fear or awareness of any object in its environment save the light which it so strenuously seeks. Its excitement increases the longer it is operated with, and after a time it may be picked up without feigning death, or with only a momentary feint."

Diligent search in the streams and ponds in the vicinity of Cambridge failing to disclose any of these animals, several dozen specimens were procured from Ann Arbor, where Dr. Holmes obtained his, and where they are often very abundant. They were shipped to Cambridge in a small tin pail, with barely enough water to cover them, but arrived in good condition and were kept in aquaria in the laboratory for a number of weeks. They were fed occasionally on *Asellus* and whatever small water beetles or other aquatic insects could be obtained, and when the freezing of the ponds made such food difficult to obtain, it was found that mealworms (*Tenebrio* larvae) could be substituted with apparently as good results. These were offered to the *Ranatras* in a pair of tweezers, usually having been crushed slightly in order to make it easier for the bugs to insert their beaks through the hard outer covering of the larva; otherwise the *Ranatras* were often unable to penetrate the larvae anywhere unless they chanced to find the soft integument at the bases of the legs. Holmes gives, in addition to a description of their reactions to light, a good account of their general habits, a knowledge of which is always an invaluable preliminary to experimental work upon any animal.

Comparatively few preliminary experiments were necessary to confirm the majority of Holmes's results, including the death-feigning, the head movements and swaying movements in response to light, and the subsequent positive phototropism, as well as the negative response to light under certain conditions. This negative response was found, in part, to occur at times when there appeared to be no definite assignable cause; but in general it seemed to be due to an appreciably less active condition, brought about possibly in many cases by exhaustion or by lack of food. As Holmes says (:05*, p. 317): "The negative reaction is associated with a condition of lowered phototonus. It is rarely shown except when the animal is in a condition of comparative sluggishness. When in great excitement, when its movements take place with quickness and vigor, *Ranatra* always shows a positive reaction." He found that the negative reaction usually followed prolonged exposure to darkness. At times, however, temporary periods of negative response appear in animals which are otherwise uniformly responding positively to light, under apparently similar conditions and with no obvious cause. It will readily be seen how this might be a disturbing influence in the experiments testing the responses to both lights; for, whereas a positive animal might be expected to turn toward the large light, if it discriminated between the two lights at all, conversely an animal in a

condition of negative response would under similar circumstances turn toward the smaller light. For this reason, although it would not matter in testing the reactions of the animal to the two lights, whether it were positive or negative, it is exceedingly important that the insect should be in one or other of these states and remain so without change throughout the experiment. It is so much easier to keep *Ranatra* in the positive condition than in the negative one, and the insect reacts so much more definitely and decidedly when positive, that, so far as possible, only individuals in this condition were used. A number of specimens were taken from the water and placed on the table. Most of them immediately went into the death faint, as described by Holmes; but there were usually a few that remained active. Some of these were occasionally positive, though more often they were negative and began crawling away from the light. After a time the others began gradually to come out of their death faint, and these, in nearly all cases, were positive. They were allowed to crawl toward the light until they became fully active and could be picked up and handled without fear of changing their reactions. That individual was then selected for experimentation which appeared most strongly and persistently positive. If, as often happened, they reached such a state of excitement that they attempted to fly to the light, the method adopted by Holmes to prevent this was resorted to, namely, fastening down their wings with asphalt varnish.

No regular separate series of experiments were made to test the reactions of *Ranatra* to the lights singly, but trials of this kind were made from time to time in the course of the tests with both lights by screening off one or the other, and exposing the animal to the remaining light. Furthermore, the method used for bringing the animals into normal orientation at the beginning of each trial afforded a means of observing immediately any change in the character of the reactions. The preliminary orientation was accomplished in the following manner: Two runways were constructed by tacking strips of pasteboard, painted black, to the sides of wooden blocks on each of which was mounted a small incandescent lamp (Figure 14, *l*, *l'*) registered as 2 c. p. By means of a single switch, either of these lamps could be lighted at will simply by throwing the switch handle one way or the other. When the switch was midway, both lamps were thrown out of circuit. If it is now desired to test an animal to the action of two lights, *Lg* and *Sm*, having it first headed north, so that *Lg* is to its left and *Sm* to its right, the animal is picked up by its breathing tube and dropped into the runway *So* with its head pointing toward *No*. The switch has pre-

viously been thrown so that lamp *l* is lighted, and the animal, being positive to light and protected from lights *Lg* and *Sm* by the sides of the runway, starts crawling straight ahead toward *l*. As soon as its head emerges from the runway it comes under the influence of the lights at the sides, and the lamp *l*, which was used only to bring it out in proper orientation, is immediately switched off. If the animal now turns toward either of the side lights, the record is taken, *Lg* or *Sm*, according to the way it turns, the record not being taken, however, until it has crawled far enough to cross the outer (15 cm.) circle. Should it go straight ahead and enter the opposite runway, the record is indifferent, or 0. The next trial is made from the other runway, *No*, and so on alternately, the specimen being headed first in one direction and then in the other, in order to avoid the possible establishment of a habit of turning in the same direction. The likelihood of this occurring without proper precaution is indicated by Holmes's work (:05^a, p. 336). Still further variation in operation was obtained by occasionally running two successive trials in the same direction, thus shifting the order of alternation.

A varying number of trials were made with 12 different individuals, the results of which are summarized in Table VII.

The results of the trials with the single lights, which were made from time to time, are included for comparison with those to both lights, since they can with considerable accuracy be taken as a measure of the positive phototropism of the animal during the period it was being experimented with. A test in each of the two orientations was usually made with each of the lights separately at the beginning of the work with any individual. The insect was then tested with both lights for

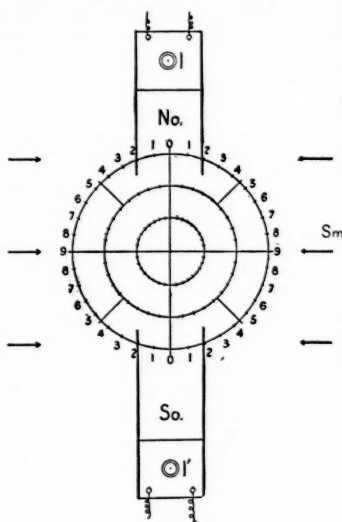


FIGURE 14. Apparatus employed for orienting *Ranatra*; *l*, *l'*, 2 candle power incandescent lamps; *No*, runway on north side of working position; *Sm*, side directed toward small light; *So*, runway on south side of working position.

TABLE VII.

SUMMARY OF REACTIONS OF *Ranatra* TO LARGE LIGHT ALONE, TO SMALL LIGHT ALONE, AND TO BOTH LIGHTS USED SIMULTANEOUSLY.

Lights used.	Large.			Small.			Both.			Total of Trials with each Individual.
Direction of Reaction.	Lg(+).	0	Sm(-).	Lg(-).	0	Sm(+).	Lg.	0	Sm.	
Individual a	4	4	6	..	2	16
" b	10	8	23	2	11	54
" c	8	1	7	23	..	5	44
" d	25	..	7	7	..	21	23	..	19	102
" e	18	1	1	3	1	20	77	14	17	152
" f	4	4	59	..	13	80
" g	7	..	3	4	..	6	23	..	5	48
" h	12	12
" i	4	4	35	2	13	58
" j	2	2	3	2	3	12
" k	6	..	2	8
" l	4	4	46	2	28	84
Totals	86	1	11	14	2	80	336	22	118	670
Per cent of total trials	87.8	1	11.2	14.6	2.1	83.3	70.6	4.6	24.8	
Excess (per cent)	76.5	68.7	45.8			
Total of trials under each condition	98			96			476			670

a considerable number of trials ; then tests were again made with the lights singly. This was not altogether necessary, since a change in the phototropic state of the animal could usually be told at once by its behavior in the runway. As it became negative, instead of going out toward the incandescent light in the other runway, it would attempt

to turn about and go from it. Furthermore, whenever an animal was subjected to both lights and turned for a number of times toward the small one, it was immediately tested with the lights separately to find whether it reacted negatively under these conditions. This was found to be the case in enough instances to establish pretty thoroughly the conclusion that a change in the character of the animal's reactions was usually an explanation of a number of turnings to the small light. The negative condition, however, often appears to be very temporary and vacillating, and at such times the animals show much hesitancy in their reactions, sometimes heading first toward one light and then toward the other, as if undecided in which direction to go. When a specimen appeared to have become at all permanently negative in its reactions, the experiments with it were discontinued and another individual was taken in its place. It will be observed in Table VII that the per cent of plus reactions for the large light and for the small light were nearly equal, — 87.8 per cent for the one and 83.3 per cent for the other, — averaging about 85 per cent of the total number of reactions in the two cases. The excess of positive over negative reactions was 76.5 per cent and 68.7 per cent respectively. When both lights were used, the per cent of responses to the large light was somewhat smaller, but still comparatively large. This was 70.6 per cent of the total number of reactions, or 45.8 per cent in excess of the reactions to the small light. These figures are considerably smaller than the corresponding ones for Vanessa, in which, it will be recalled, 87.2 per cent of the reactions were toward the large light, while the excess in that direction was 75 per cent of the whole. This difference, however, is probably caused not so much by an inferiority of the eyes of Ranatra, in respect to image-formation, as by the variable character of its phototropic states. Ranatra has periods of negative phototropism, whereas Vanessa appears never to be negative in any of its locomotor responses to light.

From the experiments which have just been described, it is apparent that Ranatra is able to discriminate between a very small source of light and a luminous area 41 cm. square, even when the intensity of the light striking the two eyes is the same; and judging by the large per cent of reactions toward the large light by animals which are positive in response to unilateral illumination, it is reasonable to infer that the eyes are capable of forming images of considerable definiteness. Differences in the normal phototropic responses of the two animals, as well as the influence of different inhibitive reactions, and other factors, will not allow the drawing of very close comparisons between the relative capacity of image-formation in the eyes of Vanessa and Ranatra. Other things being equal, the foregoing results would indicate a more precise

condition in Vanessa, but the uncertain elements which have been mentioned must be taken into account before conclusions can be drawn with any degree of confidence.

Mention has been made of individuals which at times showed much hesitancy in these reactions, and having turned toward one light seemed disturbed by the other, which was now behind them. At such times the head was usually held high, in the manner described by Holmes (:05^a, p. 312), when the light was moved to a position behind the animal. It was found that by painting over the posterior half of the eyes, so that the light was excluded on that face, the influence of the light behind the insect could be prevented. After having their eyes treated in this manner, even individuals which had previously shown great hesitancy held their heads low, and once oriented toward either light, crawled straight on in that direction without turning. This was not resorted to, however, in any of the trials summarized in Table VII. If the eyes were painted on their anterior halves, exactly the opposite state of affairs was brought about. In this way individuals which had previously shown no hesitation when once oriented toward either light, were caused to turn first to one and then to the other, the reason being that, as soon as the animal was facing one light, that one could no longer be seen on account of the paint, while the other, shining on the unpainted posterior half of the eyes, caused the insect to turn from the apparent darkness ahead to the light behind. In this way it was kept turning about and about, and making no definite progress in any direction.

8. *Pomace Fly* (*Drosophila ampelophila* Loew).

Upon this form and the succeeding one, only negative results were obtained as regards the question of inferred image-formation. It was expected from their general behavior toward light that these animals would be eminently suitable for this investigation, and the failure to obtain definite results with them was a disappointment. Long series of experiments were tried both with these flies and with snails, involving much time and labor; a brief account of them is given here merely to illustrate how certain unforeseen conditions may influence the reactions of an animal in ways entirely unexpected.

In his investigations upon the reactions of *Drosophila*, Carpenter (:05) found that this little fly is always positive in its reactions to light, at least in its locomotor responses.⁷ It, like Vanessa, often

⁷ There are undeniably times when *Drosophila* may crawl away from the source of light; but this is probably in response to other stimuli, such as food,

comes to rest with the head directed away from the light, but Carpenter does not consider this an indication of negative phototropism. His explanation is that "The fatigued insects remain quiet in this position because it is the one in which the least light enters the eyes, and in which, as a consequence, the kinetic stimulus is least" (p. 170). The desirability in the present instance of having animals which were actively phototropic and in which the character of the response, whether positive or negative, remained constant, has already been mentioned. The pomace fly seemed to fulfil these conditions remarkably well, since it is always, when in motion, positive to light, and can usually be put into motion by slight mechanical agitation whenever it shows a tendency to come to rest.

All this works out very well with a single light, but in using both lights the difficulty arises of getting the flies properly oriented at the beginning of the trial. If they chance at the beginning to be headed toward either light, they appear to continue crawling in that direction, heedless of the other light and indifferent as to whether the one toward which they are headed is the larger or the smaller. The plan was first tried of liberating a number of individuals in a box through a hole in its bottom, the box being provided with glass sides, one directed toward either of the lights. When once they alighted on either glass, they crawled upward, in consequence of their natural negative geotropism, and so passed into a trap device at the top, where they could be counted at leisure. It was expected that when they were placed in a small dark box beneath the hole in the bottom of the one with the glass sides, they would at once fly upward from the dark into the light of the upper box, and so would become suddenly exposed (as they flew upward, and oriented at random) to the influence of the large and small illuminated areas. It was found that on the contrary few of the insects flew out; the most of them crawled up over the edges of the opening and proceeded to crawl on in the direction in which they chanced to be oriented. Furthermore, a large proportion of them evinced a decided tendency to settle down and remain quiet soon after getting out into the light, coming to rest here and there all over the bottom, top, ends, and the glass sides of the box, and it took more than moderate jarring of the box to get them started to crawling again.

Next, the plan was tried of placing backwardly projecting strips of paper around the opening, making it more difficult for the flies to crawl out at the edge of the opening. At the same time there was placed

which for the time inhibit or overcome the natural phototropic reaction, and is not to be considered an active negative reaction to light.

in the middle of the opening a small wooden cone, up which the flies could easily climb. Nevertheless many still persisted in crawling out at the edge of the opening in spite of the obstructions, while those that climbed the cone usually came to rest on its sides instead of climbing up to its apex and flying thence as it was hoped they would do. Obviously, too, those which climbed the sides of the cone were often shaded from one or the other of the lights by the cone itself, and this introduced another chance for error. Finally, an outer paper cone was so arranged as to make it impossible for the flies to come out anywhere except through an opening at its apex, from which there led a narrow Y-shaped paper, one arm extending toward the large light, the other toward the small, with strings leading upward to the traps on either side. But even with this apparatus the tendency of the flies to continue crawling up the edge of the Y upon which they happened to emerge appeared to overcome in large part their reaction to light. With a single light — the large one — only about twice as many individuals went toward the light as in the opposite direction; and when both lights were used the readings were almost equal — 222 to 226.

From these results it will be seen that, although the eyes of *Drosophila* would, from their structure, appear to be as well adapted to image-formation as those of either of the other adult insects employed, the experiments with the two luminous areas of different size furnish no data whatever to aid in the determination of this point.

9. Garden Snail of Europe (*Helix pomatia* Linn.).

These snails, during the winter months when they have withdrawn into their shells for hibernation, are imported into this country by certain French restaurants in the larger cities, and may in this way be readily obtained in the living condition. Under the influence of warmth and moisture they emerge and live well, so that they may be kept in the laboratory for a considerable period. A few preliminary experiments tried with them seemed to indicate that they were for the most part decidedly positive in their reaction to light, often turning to it at once at a sharp angle. This led to the hope that they might be suitable for experimentation in regard to the effect of the two lights. The snails were allowed to crawl on the ground-glass plate in the same manner as described for the earthworm and land planarian. They are easily handled by the shell and can be placed in any position desired. As in the case of the other forms, they were first oriented in the "normal" position in the shaded area between the screens and then

allowed to crawl out into the light. Trials were made alternately with the animals headed in one direction and then in the opposite.

It soon became apparent that these snails were by no means uniformly positive to light, so it was necessary each time to test them first with a light at one side only in order to be certain of the state of the animal. It was furthermore found that they appeared to become fatigued very quickly, and apparently this was often accompanied by a change in the character of the phototropic response. Finally, the method was adopted of making only a few trials with each individual each day. The first trials were made with both lights, one trial in each of the two orientations, and then trial was made with a single light to ascertain whether the response was positive or negative to that. The records for animals that were positive were kept separate from those of animals that were negative. The responses were so irregular and apparently so dependent upon the physiological state of the animal that no very definite conclusions could be drawn. As far as they showed anything, however, they seemed to indicate a fairly indifferent reaction to the two lights in the case of animals that were negative as well as in those that were positive. This leads to the inference that the eyes of the snail do not aid greatly, if at all, in the discrimination of two lights differing in area as the two used. If, as is maintained, the general integument is sensitive to light-stimulation, a result similar to that obtained in the reactions of the earthworm to the influence of light on the skin would be expected, since, without the eyes, the condition would be comparable to that of the earthworm. These experiments on the snail, as far as they go, point to the conclusion that the ability to discriminate differences in the size of luminous areas is aided but little, if at all, by the eyes.

10. *European Garden Slug (Limax maximus Linn.).*

A few experiments were also made with the slug *Limax maximus*, as an example of a mollusk normally negative in its reaction to light. As in the case of *Helix*, however, the animals were found to be so inconstant in their responses that it was exceedingly difficult to obtain consistent results from them. Frandsen (: 01), in his work on the reactions of *Limax* to direction stimuli, found much individual difference in the reactions to light, as well as to gravity. Furthermore, he found that the reactions of the same individual vary in intensity, and even in character, with variations in the intensity of the light, and probably also in response to undeterminable physiological states. These variable conditions introduce so many elements of un-

certainly that *Limax*, like *Helix*, is unsuitable for use in experiments where constancy in the character of the reactions is necessary.

11. *Cricket Frog (Acris gryllus Le Conte).*

In the search for animals with the type of eye often known as the "camera eye" which could be employed in these experiments, the choice appeared to be rather limited. Of the vertebrates which could be used out of water most appear to be either indifferent to the action of directive light, or else their reactions are of such a complex nature that the natural responses to light are inhibited by other external stimuli or by fear. Certain of the amphibia appeared most promising, especially the frog, this animal having been experimented upon by Graber ('84) more than twenty years ago, and by a number of observers since that time. Two recent papers, one by Parker (:03*) and the other by Torelle (:03), treat rather fully of the reactions of frogs to light. Parker's observations relate exclusively to the leopard frog (*Rana pipiens* Gmelin), while Torelle used this species and the green frog (*R. clamata* Daudin) indiscriminately.

In previous years, at Ann Arbor, Mich., I had incidentally noted the marked positive phototropism of the little cricket frog, which is abundant about ponds and lakes and in the marshes of that region. It is an active little animal, capable of making leaps to a distance of a meter or more. Specimens placed on a large table top above which swung an electric light at a height of a half-meter or so were observed to make long leaps toward the light. They usually missed striking the globe, seldom going so high, and landed on the other side of the table headed away from the light. Ordinarily they would remain in this position for a short time, then turn around so as to face the light again, and then, after another interval, again leap toward it; this proceeding would be repeated until a chance jump carried them completely off the table on to the floor. The decisiveness and persistence of the reaction suggested that this animal might prove even better to work with than the common species of *Rana*. In consequence, through the kindness of friends in Ann Arbor, several dozen specimens of *Acris* were obtained from that place for the purpose of these experiments. In the meantime a number of other amphibians, including two species of *Plethodon* and *Diemyctylus viridescens*, were tested as to their light reactions, but although these in general appeared to be negative to light, as would be suspected from their habits, their reactions to the intensity of light used did not appear sufficiently marked to make them suitable for these experiments.

In the experiments with *Acris* the animal was placed beneath a small glass box (approximately 4 cm. \times 5 cm.), large enough to allow the frog to turn freely in any direction but not permitting it to hop any distance. Care was taken to keep the sides of this box normal to the directive axis of the apparatus, and although the intervention of the glass between the animal and the light on each side introduced reflections which could not be avoided, it appeared, from certain tests that were made, that these were sufficiently insignificant to be disregarded. The method of orienting the animals at the beginning of each trial, at right angles to the line joining the two lights, was similar to that employed in working with *Ranatra*. When it was desired to start with the frog headed north, for example, a small incandescent light was turned on at that side, while screens were placed between the animal and the experimental lights. Under these conditions the frogs usually turned within a short time and faced the incandescent lamp. This got them into the desired position, so that the incandescent lamp was then turned off and the screens removed as nearly simultaneously as possible, leaving the frog exposed to the influence of the large and small lights, one at either side. The next trial was made in precisely the same way except that the incandescent lamp was placed to the south instead of the north, and in consequence the frog was oriented in exactly the opposite direction to what it was in the previous trial.

Four series of experiments, comprising in all 300 trials, were made upon the reactions of *Acris* to the two lights. The first three of these, (Table VIII, *A*, *B*, and *C*) were made with the lights at the same distance that had been used throughout all the experiments, namely, at 2 meters from the animal, or 4 meters apart. As has already been stated (p. 345), this gave a light intensity of 1.25 to 5 C.M. falling upon the animal on each side. The combined results of these three series are given in Table VIII. Before making series *D*, which is similarly summarized in Table IX, the lights were moved nearer together until they were but 2 meters apart, thus reducing the distance between them and the animal by half and increasing their intensity at that, the median, point four times. The intensity of light striking each side of the animal was consequently then about 5 C.M. to 20 C.M. With the stronger intensity the frogs reacted much more quickly and uniformly. They sometimes acted almost immediately when the orienting light was turned off and the screens removed exposing them to the experimental lights; but usually there was an interval varying from a few seconds to half a minute, or even longer, before they turned toward one light or the other. Parker (: 03*, p. 29) found similarly that *Rana pipiens* responded much more quickly to the stronger light intensities. At the

TABLE VIII.

REACTIONS OF *Acris gryllus* TO BOTH LIGHTS.

Series.	Date.	Individual.	Turnings to Lg.	Turnings to Sm.	Total Trials.	Remarks.
A	May 14	1	10	0	10	Inactive. Apparently not strongly +phototropic. Turned in all cases to its left.
	" "	2	7	3	10	
	" "	3	9	1	10	
	" "	4	7	3	10	
	" "	5	3	7	10	
	" "	6	7	3	10	
	" "	7	5	5	10	
	" 15	8	4	6	10	
	" "	9	4	6	10	
	" "	10	7	3	10	
B	" 25	1	3	1	4	Very inactive. Not strongly +. Turned always to its left.
	" "	2	2	0	2	
	" "	3	1	5	6	
	" "	4	2	2	4	
	" "	5	3	1	4	
	" "	6	3	1	4	
	" "	7	4	0	4	
	" "	8	4	0	4	
	" "	9	2	2	4	
	" "	10	2	2	4	
C	" 26	1	4	0	4	Seemed quite strongly +. Turned always to its left. Turned always to its left. Strongly +. Reactions prompt.
	" "	2	1	3	4	
	" "	3	4	0	4	
	" "	4	2	2	4	
	" "	5	2	2	4	
	" "	6	2	2	4	
	" "	7	3	1	4	
	" "	8	3	1	4	
	" "	9	3	1	4	
	" "	10	4	2	6	
	" "	11	4	0	4	
	" "	12	3	1	4	
	" "	13	3	1	4	
	" "	14	2	2	4	
	" "	15	1	1	2	
Totals			130	70	200	

lower intensities used by him (in the neighborhood of 1 C.M.) "the animals often did not react for from five to ten minutes or even longer." It was only an exceptional specimen of *Acris* that did not react within less than about a minute, and as the intensity of light employed was not far from the lower intensities used by Parker, it is obvious that,

TABLE IX.

REACTIONS OF *Acris gryllus* TO BOTH LIGHTS AT HALF THE CUSTOMARY DISTANCE.

Series.	Date.	Individual.	Turnings to <i>Lg.</i>	Turnings to <i>Sm.</i>	Total Trials.	Remarks.
<i>D</i>	May 29	1	4	0	4	
	" "	2	8	0	8	Turned toward <i>Lg.</i> , even if facing at first more toward <i>Sm.</i>
	" "	3	7	1	8	
	" "	4	3	5	8	
	" "	5	8	0	8	
	" "	6	7	1	8	
	" "	7	8	0	8	Strongly +; reactions very definite.
	" "	8	8	0	8	
	" "	9	8	0	8	
	" "	10	7	1	8	Did not orient well to single light. Apparently — part of time. At first +; then became —.
	" "	11	5	3	8	
	" "	12	4	4	8	
	" "	13	6	2	8	
Totals . .			83	17	100	

as judged by the time required for response, *Acris* is much more sensitive to this form of photic stimulation than the leopard frog.

An inspection of Table VIII will show that out of 200 trials 130 (65 per cent) were toward the larger light, an excess of 30 per cent in that direction over those in the opposite direction. The proportion of turnings to the large light is undoubtedly considerably lowered by the inclusion of several individuals which appeared to be indifferent or

defective in their reactions, such as No. 7 in Series *A*, and Nos. 4 and 6 in Series *C*, which turned in all cases to their left. This may have been due to indifference to light, the animals turning to their left possibly for some structural reasons, or there may have been some defect of sight in the right eye, which would also result in a turning always to the left. It should be mentioned that the same individuals, in part at any rate, were used in the different series, but that the numbers by which they are designated in the various sets do not correspond. For this reason No. 4 or No. 6 of Series *C* may have been the same individual as No. 7 of Series *A*, but it is impossible to say definitely. It was found, too, that sluggish or inactive individuals, or those which did not orient readily to the light used for that purpose before making the trial, gave in general a much smaller proportion of reactions toward the large light than those frogs which reacted promptly and oriented readily to the incandescent lamp. Individuals No. 5, Series *A*, and No. 9, Series *B*, are examples of the inactive sort.

Series *D* comprised 100 trials, on 13 different individuals, with the lights at half the usual distance. The results are shown in Table IX, and are so decided as to admit of no doubt as to the character and meaning of the reactions. Of the 100 trials, 83 were toward the large light and only 17 toward the small one. This means an excess of 66 per cent of the turnings in the direction of the large light. This is considerably larger than the corresponding value found for *Ranatra* (45.8 per cent; cf. p. 387), but smaller than that found in the reaction of *Vanessa* (75 per cent; cf. p. 382). It will be noticed that with the exception of individuals 4, 11, and 12, all the animals turned toward the large light in at least three-fourths of the trials with them, that is, in at least 6 out of 8 trials; and if the records of these three had been omitted, it would have brought the total number of reactions toward the large light up to 93 per cent, or an excess of 86 per cent over those in the opposite direction. No memorandum appears to have been made at the time with regard to the behavior of individual 4 in other respects; but No. 11 "did not orient well to single [incandescent] light" and was "apparently negative," at least part of the time; while No. 12 was "first positive, then became negative." In correspondence with this change of behavior to a single light in this last individual, it first gave 4 turnings to the large light and then 4 to the small.

It will thus be seen that the proportion of reactions to the large light by *Acris* was considerably lowered by the inclusion of the records of these three animals, which were either in a negative, or at least an inconstant or indifferent, state as regarded the character of their responses to one-sided illumination. As with *Ranatra*, this

inconstant and not accurately determinable factor precludes making direct quantitative comparison with the results obtained upon Vanessa or other forms. If such a comparison were to be attempted, it would probably be justifiable to leave out of account entirely the results on the three specimens of Acris which appeared to be negative, since Vanessa appears to be always positive, and the comparison would then be between animals which were in similar constant phototropic states. If such were done, the proportion of turnings to the larger light would be greater for Acris (as based on Series *D*) than for Vanessa, and in so far might perhaps be interpreted as indicating the formation of more distinct and better images of the lights on the retinae of the former than the latter.

Parker (:03*) proved that *R. pipiens* is as a rule positively phototropic to stimuli received by the skin, as well as to those received by the eyes. The idea suggested itself of using Parker's methods and testing in Acris the effect of the large and small lights when falling (a) upon the eyes alone, the skin being protected from the light, and (b) upon the skin after the optic nerves had been cut. If the persistent turning of the normal frog toward the large area of light was to be attributed to the ability of the eyes to form images of the lights, it would be expected that frogs with the skin protected from the light would still react as before, so long as vision with the eyes was unimpaired. On the other hand, an eyeless frog — or what amounts to the same thing, one in which the optic nerves had been severed — might be compared directly with an earthworm, so far as its light-perceiving abilities are concerned. It has only the general integument for the reception of photic stimuli, and while, as in the earthworm, this is undoubtedly sensitive to differences of intensity, there is no more reason to suppose that it would enable the animal to discriminate between different areas of like intensity but unequal size than in the case of the worm.

In making the test with the eyes exposed and the skin covered the method employed by Parker was followed in detail. The skin was removed in one piece from a large, dark-colored individual, turned inside out, and drawn over a slightly smaller specimen which was known to be active and strongly positive in its reaction to light. In addition to the eyes, the snout and fore and hind feet were exposed to the light. Only a single individual was used for this test, but the nature of its responses was so decided that further experiments did not seem necessary. When exposed as the normal frogs had been, to the influence of the two lights, it turned toward the larger in 11 out of 14 trials, about as large a proportion as was obtained with normal animals. The frog was much slower in its reactions than it had been previous to

having the skin of the other specimen slipped over it, not responding within two minutes in more than half of the trials, so that it had to be started by mechanical stimulation. As a check experiment, the enveloping skin was now drawn forward so that it covered the eyes as well as the rest of the body. The frog no longer turned toward the large light, but, on the contrary, an unexpected result was obtained; for it now turned in nearly all cases toward the smaller light, when it

TABLE X.

REACTIONS OF *Acris* AFTER THE OPTIC NERVES HAD BEEN CUT.

BOTH LIGHTS.				SMALL LIGHT.			
Individual.	Direction of Reaction.			Individual.	Direction of Reaction.		
	<i>Lg.</i>	0	<i>Sm.</i>		—	0	+
1	2	6	2	1	1	5	4
2	3	4	3	2	1	4	15
3	..	6	..	3	1	2	1
4	3	4	3	4	2	2	6
Totals	8	20	8	..	5	13	26

would have been expected to be indifferent, since both skin and eyes were protected from the light. A larger series of experiments might have explained this apparent anomaly,⁸ but by this time the specimen had become exceedingly sluggish and inactive, and it was believed that the results obtained sufficiently demonstrated that *Acris* discriminated between the two areas by means of the light from them that entered the eyes.

It now remained to test animals by exposing their skin to the full

⁸ Two possible explanations of what may have caused the results obtained suggest themselves: (1) The portion of skin covering the eye toward the small light may have been more pervious to light than that over the other eye, due to its having been stretched more tightly, to a difference in pigmentation, or possibly to injury, such as an abrasion or a small perforation; or (2) it may be that the light from a small area such as was used may have a greater penetrating power through a membrane of this character than the more diffuse light from a larger area.

influence of the lights, after their eyesight had been destroyed. This was accomplished by cutting the optic nerves, a simple operation, performed by inserting the points of a pair of fine scissors just back of the eyeball, through the membrane lining the roof of the mouth, and severing the nerve where it leaves the eye. The frogs did not seem to be greatly inconvenienced by the operation, and three of the four individuals so treated appeared to be as active as before, except that they did not respond so quickly to light. The fourth animal (No. 3 in Table X) was more sluggish and behaved much as frogs do that have had the cerebral hemispheres removed. All the specimens were so slow in turning toward the incandescent light which had been used in the previous experiments for orienting the animals into the normal position, that they were placed in the desired orientation by moving the glass plate upon which they were sitting. This could not be rotated directly to bring the frogs into position on account of the compensating circus reflex which resulted, but the plate was moved backward and forward in line with the longitudinal axis of the frog's body a distance of about 15 cm., and each time was turned slightly until the animal was finally oriented. In this way the greater part of the motion was lengthwise of the frog, and the rotating was so slight in comparison with the backward and forward movement that there seemed to be no tendency to give the compensating reflex.

Individuals 1 and 2 usually turned in one direction or the other, or hopped or walked ahead—in other words, gave some locomotor response—within 2 minutes of the time they were exposed to the lights. If not, they were stimulated by touching them from behind. As has been mentioned, No. 3 was inactive and slow to react, while No. 4 was intermediate between No. 3 and the other two. In cases where the animal hopped or walked ahead without turning at least 45° in one direction or the other the record was taken as indifferent, and is included in the column headed 0 in the table.

The left half of Table X summarizes the reactions to both lights of the four individuals with the optic nerves cut. The larger part of the records (20 out of 36) were indifferent; but it is a curious fact that each individual turned exactly as many times toward one light as toward the other. In all there were 8 turnings toward each lamp. This shows a perfectly indifferent condition, and demonstrates that *Acris* is unable to discriminate by means of the skin alone between luminous fields of different size where the intensity of the light from each falling upon the animal is the same.

In order to make certain that the skins of these animals were sensitive to light, the same individuals were finally tested with the small

light alone. The results of this test are recorded in the right half of Table X. It will be seen that each individual gave a preponderance of reactions toward the light, except No. 3, which turned once in each direction, and twice went ahead without turning. Three of the frogs were thus undoubtedly positively phototropic to light stimuli received by the skin, and the inherent inactiveness of No. 3 has already been remarked. From the totals it is seen that out of 44 trials 26, or more than half, were positive, or toward the light, 5 negative and 13 indifferent.

From the foregoing experiments it seems that the following conclusions may legitimately be drawn :

1. *Acris gryllus* is preponderatingly positively phototropic, though there is some inconstancy in the reactions of the same and of different individuals, depending upon unascertained factors.

2. Exposed to luminous areas of different size but equal intensity, it turns in by far the greater number of trials toward the larger of the two areas.

3. The result is substantially the same when the skin of the animal is protected from the light, but the eyes are exposed.

4. *Acris* deprived of sight by severing the optic nerves, but having the skin exposed to the light, is indifferent to the size of the luminous field.

5. From this it follows that the discriminating power as to the different areas lies in the eyes, and is the result, it is safe to infer, of the ability of these organs to form comparatively clear images of external objects.

6. *Acris* with the optic nerve severed is still positively phototropic, but in this case, where the light must be perceived by the skin, its condition as regards image-formation and the consequent ability to discriminate between luminous areas of different sizes is directly comparable to that of an eyeless animal, such as the earthworm.

12. *Green Frog (Rana clamata Daudin).*

A number of experiments of a similar nature to those last described were made with the green frog for the purpose of comparing its reactions with those of *Acris*. The general method employed was the same, but differed slightly in details. The frogs were placed beneath a glass box 10 cm. \times 12.5 cm. \times 10 cm. high, and an attempt was made to get them to orient in the normal position by means of the incandescent lamp, as was done with *Acris*. They were so slow in responding, however, that it was found more expedient to raise the box and

orient them with the hand. Care had to be taken to avoid a one-sided turning due to circus compensation or thigmotactic stimuli received by this act, and in order to guard against such results the animal was left sitting screened from the lights for a period of 15 seconds to 30 seconds after it had been placed in orientation; if it had not moved by the end of that time the screens were removed, exposing it to the lights from the two fields.

Rana clamata was found to be much slower in its reactions than *Acris*. It was usually given 5 minutes in which to react, and if at the end of that period it had not moved, it was induced to do so by means of an electrical stimulus applied to its lower side. This was accomplished by having the board on which the frog was placed crossed by fine parallel copper wires 1 cm. apart, alternate wires being connected respectively to the opposite poles of a single "Columbia Dry Cell No. 6." By means of a simple "key" placed in the circuit the frog sitting on the wires was stimulated by the "make" and "break" of the current whenever the key was pressed down and released. This method was used rather than simply touching the animal from behind, as it was believed that there was less chance of the stimulus being one-sided, and because no movement of the operator was necessary in the field of vision of the animal. On the whole it was found to work very satisfactorily.

The results need not be given in detail, but may be stated briefly as follows:

1. As stated by Torelle (: 03), *Rana clamata* is positively phototropic in nearly all cases at the ordinary temperature of the room (about 20° C.).

2. Such positive individuals, when exposed to the two light areas of different size, turned in the great majority of cases toward the larger light. This result agrees with that obtained with *Acris*, but as would be expected from an animal which responds less quickly and definitely to a single light, the proportion of the turnings to the large light was not so large.

3. At low temperatures (6° C. to 10° C.) the frogs were usually negative in their responses to a single light, or at least were indifferent or inconstant in their reactions; and in accordance with this

4. Such individuals turned toward the smaller of the two lights, or were inconstant and gave indifferent results under these conditions as with the single light. This last result was first obtained from a specimen which was brought into the experimenting room from a tank in which the water registered 8° C. and was at once tested with the two lights. Its first 8 reactions were all toward the small light, after which

it turned in most cases toward the larger area. Out of 32 trials following the first 8, 22 were in this direction. By the time the first 8 trials had been made the frog had been in the warm room for a half hour or more, and it seemed reasonable to assume that the change in its reactions was due to its having become warmed up to the room temperature. Further observations tended to confirm this conclusion; and this agrees with the results obtained by Torelle (:03), who says, (p. 487): "A rise in the temperature to 30° C. accelerates the rate of the positive response. A lowering of the temperature to 10° C. produces movements away from the light."

IV. GENERAL CONSIDERATIONS AND DISCUSSION.

Conclusions as to the degree of the ability possessed by the various animals studied to form images, as inferred from the results of the experiments, have been stated in connection with the description of the experiments upon each animal employed. It still remains to consider certain general phases of the subject: to examine the relationship existing between the natural habits of the animals and their reactions to the two lights; to determine, in so far as possible, what part their phototropism — especially in its relation to luminous areas of different sizes — plays in their ordinary activities; and to attempt to trace, as well as can be done with the limited data at hand, the probable steps which have led to the development of highly specialized organs capable of forming richly detailed images of external objects.

It is a noticeable fact that those forms which showed by their reactions the most evidence of discrimination between the two lights (viz., Vanessa, Ranatra, and the two species of frogs) are all positive in their ordinary phototropic responses. On the other hand, the earthworm, the land planarian, the mealworm, the sow bug, and the cockroach — all of which showed little or no ability to discriminate between the different areas, but responded almost entirely according to the relative intensities of the lights — are all ordinarily negative. When one remembers that all the animals in the second group live either in the ground, or beneath stones, logs, or similar objects, or in other dark places, the nature of their responses is not surprising. For, whatever view may be held as to the way in which adaptation may have come about, it is undeniable that organisms are adapted to their ordinary conditions of life; consequently it would not be expected that those which live in darkness, or in very dim light, would be so likely to be provided with image-forming organs, since for these they would have little or no use. The ability to distinguish light from darkness is,

however, important to them, since it aids them in remaining concealed, and is thus of service in protecting them from enemies to which they would be exposed if they came into the light, and in preventing them from going into situations that would be unsuitable in other respects (lack of moisture, etc.). The negative reaction to light is not, however, the only form of response to change in environmental conditions which operates to keep these animals in their accustomed habitats; responses to contact stimuli, to moisture, temperature, and other variable conditions, are often undoubtedly of as much, if not, indeed, of greater importance. Such, for example, must be the case, as pointed out by Loeb ('90, p. 51), in the larva of the willow-borer, which lives in a dark situation, but is, nevertheless, positive in its reaction to light when exposed to its influence. It is not necessary to enlarge upon the advantages which the ability to perceive distant objects (i. e., those with which the organism does not come in direct contact) in their proper spacial relation gives to animals living in the light. An organism, by means of what we ordinarily speak of as "sight," is brought into close relation with a part of its environment which organisms wanting this faculty have no means of appreciating. This obviously is of distinct advantage. As the converse of what has just been said about dark-inhabiting forms, it may be expected that those normally living in the light are as a rule positively phototropic, and this seems in general to hold true. Where a change in the character of the phototropic response takes place, — as is the case in many animals which are under certain conditions positive and under others negative, — it is probable that this change can in most cases be explained by the natural habits of the animal. Different factors may operate to bring about this change of reaction; it may be mechanical stimulation, a variation of temperature, or a change in the intensity of the light itself. The result, in many cases at least, is to bring the organism into an optimum condition, either as to light intensity or some other stimulus. The frog (*Rana*), for example, becomes negative to light at temperatures below 10° C., and this response is probably an important one under natural conditions in inducing the animal to swim downward to the bottom of the pond and bury itself on the approach of cold weather.

We do not need to concern ourselves at this point with the theories as to how this adaptation has come about. It is sufficient to show that such adaptation exists. It may be asked whether certain animals have become negatively phototropic because they live in dark places, or whether they live in dark situations because they are negative in their reactions to light. The two probably have developed together.

An animal is dependent upon certain reactions to its environment to keep it in the proper conditions for its best welfare, and in many cases the response to light is without doubt of great importance in this respect. It is questionable whether a *Bipalium*, for example, were it positively phototropic, could long survive unless it had developed in addition to its phototropism some other form of response that would prevent its going, under the influence of the light, directly into the most unfavorable conditions. Loeb ('90, p. 51) stated that, so far as he had found, all larvae of *Lepidoptera* were positively phototropic, even including the willow-borer, which, as previously mentioned, like most negative animals, lives naturally in a situation with little or no light. It would seem that we have here a case of secondary adaptation; the willow-borer, we may infer, has become adapted to living in a dark situation *in spite* of its positive phototropism. It comes from a group of animals uniformly positive in their reactions to light, and has probably inherited this character from its positively phototropic ancestors. We have seen that as a rule animals like the earthworm and *Bipalium*, which live in dark situations, lack image-forming eyes; at least such is the inference from the responses of these forms to equal illumination from areas of different size. It has been pointed out that the possession of such eyes could be of no use to them in the dark; and it is likewise obvious that the simpler organs are equally effective in preventing the animals from straying out into the light. All that is necessary for them is to avoid light altogether. This can be done, however, with greater precision when the organism is able to appreciate more exactly the *direction* from which the light comes. The earthworm probably has little power of discrimination in this respect beyond recognizing upon which side the source of light lies, — on its right or on its left, — according to whether its right or its left side is illuminated. *Bipalium*, on the other hand, by the arrangement of many of its eyes around the anterior margin of the semicircular head, is able to determine the direction of the light more accurately, and consequently shows a quicker and more precise response by moving directly away from it. Similarly, in the mealworm, the sow bug, and the cockroach, the eyes are probably little more than "direction eyes."

The experiments on *Helix* failed to give any decisive evidence as to the ability of these animals to discriminate between the two areas. Nor do the observations of Mitsukuri (:01) and Bohn (:05) help us much in this respect, since neither of these authors discriminated between the size of the areas and the relative intensity of the light received from them. Bohn studied the reactions of *Littorina* when vertical screens, both black and white, were placed in the illuminated

field, and speaks of these animals as being "attracted" by the one and "repulsed" by the other. This terminology is rather misleading. It should be remembered that every object upon which the light falls and from which it is reflected becomes thereby a secondary source of light and must be so treated; its size is therefore of importance as one of the factors in determining the total amount of light which it reflects. If the surface is what we ordinarily term black, it reflects very little light, and its position may consequently represent the region of lowest light intensity in the whole illuminated field. A white screen, on the other hand, may reflect practically all the light that falls upon it; and if of large size, it is reasonable to predict that upon such animals as Vanessa, Ranatra, and the frog it would exert a greater influence than the source from which the light primarily came, provided the latter were of relatively small area. Thus, if the light from a projection lantern were thrown upon a large white screen and one of the above-mentioned animals were placed midway between the screen and the lantern, one would expect, from the results of the experiments performed on these species, to see the animal turn toward the large area of light, viz., the screen.

Loeb appears not to have considered in his experiments light reflected from surrounding objects, but in speaking of light coming from more than one source, he says (Loeb :05, pp. 61, 62): "When the diffused daylight which struck the [fly] larvae came from two windows the planes of which were at an angle of 90° with each other, the paths taken by the larvae lay diagonally between the two planes;" but in other places (cf. :05, p. 2, footnote) he states specifically that "if there are several sources of light of unequal intensity, the light with the strongest intensity determines the orientation and direction of motion of the animal;" in this case apparently the animal ignores the influence of the other lights altogether.

Miss Towle (:00, p. 365), in her work on Cypridopsis, found that these animals took a diagonal course due to light coming from other directions beside the main source, and decided that "the resultant direction [which the animal would take] could be found by compounding all these forces if their direction and relative value were known." The same question was later examined carefully, critically, and in an able manner, by Holt and Lee (:01); but in both these papers only the *intensity* of the various light components was considered, no account being taken, even in the theoretical discussion, of the possible influence of the *size* of the areas of the various light-sources.

In his study of Littorina, Bohn (:05, pp. 28, 29) puts the matter the other way about and uses the direction taken by the animals (their

"trajectories") as an indication of the resultant of the light forces;⁹ their paths he takes as indicating "veritable lines of luminous force." This comes very close to reasoning in a circle, and is at best merely qualitative, since he has not attempted to make a physical determination to verify his contention that the direction taken by the animals does really coincide with the resultant of light intensities. If *Littorina* responds only to the intensity of the light, we should expect that its course, in an illuminated field of this nature, would coincide with the resultant of the light intensities, could such be determined by physical measurements; but if, like *Vanessa*, it reacts differently to different areas, not in proportion to the intensity of the light received from them, but according to their extent, the direction taken by the snail would probably deviate accordingly from the resultant of intensities. It seems impossible to decide from the results either of Bohn or of Mitsukuri (:01), whether *Littorina* reacts to differences of intensity only, — the size of the screens or other objects in the field being of importance merely in determining the amount of light reflected or absorbed, and thus influencing the direction of the resultant "lines of luminous force," — or whether, like *Vanessa*, it may react to the areas according to their size, more or less irrespective of the intensity of light received from them. Whichever may be the case, Bohn (:05, p. 30) has pointed out that the shaded surfaces of rocks act in the same way as black screens, and that when a *Littorina* is in the vicinity of two such shaded areas it does not go directly toward either, but strikes a course which is a mean and eventually leads it into the crevice between the rocks.¹⁰ This is apparently another case where the reactions of the animal to light are well adapted to its needs, since the snails are undoubtedly much better protected in the crevices than they would be upon the exposed surfaces of the rocks.

To animals commonly living in the light the possession of eyes capable of forming images must be of distinct advantage. Neverthe-

⁹ "En un point donné d'un champ lumineux la direction du champ n'est que la direction de la résultante de toutes les forces attractives et répulsives exercées par les surfaces éclairantes, surtout par les surfaces les plus étendues, les plus hautes (fenêtres, murs)."

¹⁰ "Chaque surface d'ombre exerce une attraction proportionnellement à son étendue, et l'animal suit une direction qui est celle de la résultante des forces attractives. En particulier, quand une littorine se trouve dans le voisinage de deux rochers présentant des surfaces d'ombre d'étendue par trop inégale, elle prend une direction qui est celle de la diagonale du parallélogramme des forces attractives, et ainsi il lui arrive de se mouvoir vers un espace compris entre les deux rochers et de ne rencontrer ni l'un ni l'autre, bien qu'attirée par l'un et par l'autre."

less, there are numerous examples of positively phototropic forms whose reactions to light tend to carry them always into regions of greater illumination, but whose eyes are probably of little use beyond determining the direction and the relative intensities of lights. Here, again, there appears to be a correlation between the habits of the animals and the conditions under which they live, for an inspection will show that these are usually creeping forms whose movements toward the light take them in the direction of their food, or else that other conditions prevent their phototropism from taking them into unfavorable surroundings. The caterpillars of *Porthesia* (and probably of most other *Lepidoptera*) may be taken as an example of the former. Although no tests have been made on these forms to determine their ability to discriminate between luminous areas of different size, the rudimentary condition of their eyes, and the experiments with beetle larvae (*cf.* *Tenebrio*) make reasonable the assumption that they respond only to the intensity of the light reaching them, and not to the size of the area whence it immediately comes. Under ordinary conditions, in the sunlight, the largest patches of light are on the ground; but the strongest intensity is skyward, and responding to this, as soon as hatched, the young caterpillars of *Porthesia* crawl upward and outward on the branches until the reaction to food overcomes their phototropism, or they are prevented from going farther by reaching the tips of the branches. In these two ways their progress skyward is checked at the proper time. In a similar manner positively phototropic snails or other crawling forms are restrained by the natural conditions from continuing indefinitely their migrations in the direction of the greatest illumination. Parker (: 03, p. 462) has called attention to the fact that the surface of the water forms a similar barrier to certain marine organisms (such as the copepod *Labidocera*) which swim upward through the water toward the light.

With forms which fly, and so, being independent of solid objects upon which to crawl, are not limited in the distance which they might move upward, the case is entirely different. A query which Romanes ('83, p. 279) found among Darwin's manuscript notes shows careful observation and puts the question very clearly. It is as follows: "Query. Why do moths and certain gnats fly into candles, and why are they not all on their way to the moon — at least when the moon is in the horizon? I formerly observed that they fly very much less at candles on a moonlight night. Let a cloud pass over and they are again attracted to the candle." Romanes thinks the answer is that "the moon is a familiar object, the insects regard it as a matter of course, and so have no desire to examine it." As a result of Parker's work on *Vanessa* and

those of the present investigation, however, we are able to give another and, it would seem, a more reasonable explanation. The moths and gnats referred to react, like Vanessa, to large areas of light rather than to a point of more intense light. As a consequence they remain near the ground, on account of the bright patches of moonlight, instead of flying toward the moon itself. If, however, they come close to a candle, its relatively great intensity at so short a distance may overcome the reactions to the moonlit areas, and the insects accordingly fly into the flame. This is especially the case, as recorded in the note, when the moon is obscured by a cloud and the patches of moonlight disappear.

Parker (:03, p. 461) has pointed out, furthermore, that the alighting of Vanessa in sunny spots with the wings expanded is probably an adaptation which serves to bring the sexes together; for it is in this position, headed as it always is away from the sun, that the colors and markings of the upper surfaces of the wings are most conspicuous. He adds, "I am sure from direct observations that females, as well as males, will circle around an oriented and expanded individual of either sex, till both fly off together." The recognition by one butterfly of another as a definite object in its field of vision indicates a much finer perception than that which distinguishes merely the difference of size in illuminated areas, and approaches to the highest type of vision. Although no experiments were made which bear directly upon this point, it is, nevertheless, worthy of brief consideration.

Nuel (:04) speaks of "la perception simultanée des fins détails des objets visuels" as "iconoperception" (p. 82), and of the resulting reactions as "icono-réactions."¹¹ He says (p. 83): "Chez les animaux, nous ne parlerons pas d'iconopsie, mais d'icono-réactions, dans la cas où, comme chez l'homme, des mouvements sont suscités ou guidés, réglés par les fins détails visuels des objets." As the perception of the details of the objects in the general image of the visual field becomes more refined, the reactions to these objects, or to certain particular ones of them, appear largely to inhibit the reactions to light in general, including that to large areas as contrasted with small. Besides the case of Vanessa, mentioned above, it seems certain that many Lepidoptera and bees react to certain flowers, while many predacious insects, such as the dragonflies, are remarkably quick in detecting their prey. That color is not, in all cases at least, the determining factor in

¹¹ The words *iconotropism* and *iconotaxis* would correspond with the terms more generally employed, such as *phototropism* and *phototaxis*, and might be employed to designate specifically the reactions of animals to areas of light and to objects in the field of vision, in contradistinction to reactions to the intensity of the light.

these responses, is indicated by such observations as that of Latter (:04, p. 88), who "once observed a brimstone butterfly visiting flowers of the Dog Violet scattered along a bank, and picking out these flowers to the exclusion of all others with great precision, not approaching even other blue flowers that were present." The description of the feeding of *Ranatra* by Holmes (:05², p. 325) furnishes an excellent illustration of the inhibition of the ordinary phototropic responses by attention to particular objects in the visual field. Holmes's description is as follows: "The phototactic response may also be inhibited by efforts to obtain food. *Ranatra* which are swimming towards the light can often be caused to discontinue their phototactic efforts if several small insects are placed near them. If the phototactic activities are very lively and vigorous, it is more difficult to divert the attention of the insect to the capture of prey. When attention is once directed to seizing the smaller insects, the light is disregarded. When the prey has once been captured and the *Ranatra* is engaged in sucking out its juices little attention is paid to the light. The repast being finished the insect may resume its positive response."

Attention to moving-objects would appear to be more general than, and probably precedes, the response to stationary objects. This is well illustrated in the feeding habits of frogs, toads, and many lizards, which seldom or never notice an insect so long as it is quiet, but are attracted by it at once if it moves. An object moving in the field of vision may, however, affect the elements of the retina in quite another way than does an object which is stationary; for, unless its color intensity is uniform with that of its background, its movement must produce a change in the intensity of the light reaching certain of the visual elements in the retina, and the response may be to this change in intensity rather than to a definite and clear-cut perception of the object as such. The question of how far animals are able to, and do, distinguish stationary objects is rather a difficult one to solve. As has just been said, it is well known that frogs react to small moving objects, such as insects, which constitute their food. It is also a matter of common observation that if a frog sitting on the bank of a stream or pool is disturbed, it ordinarily jumps at once in the direction of the water, even if it is approached from a direction parallel to the shore line. The question arises as to whether the frog recognizes the water by its appearance or whether the response is merely a reaction to a larger area of illumination. For it seems quite certain that the open water and sky on the one hand must in general form a larger area of illumination than the bank, with usually tall grass, bushes, or similar dark objects, on the other. We have seen (p. 393) that, although a frog may sit for a considerable

time in a position without apparent orientation to the light, if it is disturbed it usually turns at once and jumps toward the light; and if there are two areas of illumination of different size, it turns toward the larger. Is, then, its ordinary response of jumping toward a pool or stream to be considered as a simple reaction of this kind? It will be seen that this is similar to what, in Mitsukuri's (:01) opinion, determined the shoreward migration of *Littorinas*. A series of observations was started in connection with the present investigation in an attempt to determine the question for the frog, but as yet a sufficient number of experiments has not been made to settle the matter definitely. It need only be said that so far as they have gone, the results appear to indicate that the reaction is not so simple as has been suggested—that apparently the objects in the visual field exert an influence beyond that merely of the amount of light received from any direction, or of the size of the area from which the light is received.

In those higher animals whose actions correspond still less to simple reflexes, as acute vision (the perception of details in the visual field) becomes more perfectly developed, simple phototropic responses become more and more a secondary matter, until they appear to be entirely absent, or at least are not recognizable as such. Birds give evidence of possessing especially acute vision, and under ordinary circumstances certainly show no evidence of simple phototropic responses; but the way in which migrating birds often, on stormy nights, gather about lighthouses and dash into the glass only to be killed, recalls strongly the flying of moths into a flame, and it seems possible that this is an expression of phototropism in birds which is ordinarily inhibited by other responses.

Finally, in recapitulation, we may distinguish roughly the following four stages or types of reactions of animals to stimuli received by the photo-receptive organs.

Type A. Response of eyeless forms.

These are in general given by animals which live in dark situations and are negatively phototropic to light of ordinary intensity, though they may (e. g., earthworm) be positive to lower intensities. Some, such as *Hydra* (Wilson, '91), are positive to light of ordinary intensity. The reactions of a frog with optic nerves cut are essentially those of a positive eyeless form. Animals in this group respond only to light intensities.

Type B. Response of forms with "direction eyes."

Animals with eyes of this type also react to light intensity only, and are more commonly negative; but some of them, such as many Cope-

pod, larvae of Lepidoptera, etc., are positive; these are commonly limited, however, in their movements toward the light by physical conditions, which either bring them into favorable relations with their surroundings (e. g., to their food supply), or at least prevent their coming into unfavorable conditions.

Type C. Response to size of luminous field.

The animals which give this type of reaction appear to be usually positive to light of ordinary intensity, in which case, other things being equal, they turn toward the larger of two areas of illumination. Some of them (e. g., *Ranatra* and the frog) under certain conditions change the character of their response, and probably turn oftener to the smaller light than to the larger one, though not enough observations have been made to settle this point conclusively. It is probably only when the animals are positive that the reaction to the size of the illuminated area is adaptive.

Type D. Response to definite objects in the visual field.

This form of response includes what we ordinarily mean by the term "vision." As Nuel (: 04, p. 10) says, "Le mot 'voir' supposant généralement une distinction visuelle et une représentation visuelle et psychique des objets." The responses to definite objects are not often in the nature of simple reflexes, but are complicated by psychical processes. In most cases they inhibit direct phototropic response, which may be in evidence at certain times only (as in *Ranatra* and the frog, and possibly in birds), or may apparently be absent altogether.

In the lower forms we speak of these responses as phototropic reactions, photo-reactions, or simply reactions to light; in the higher forms, whose reactions give evidence of being governed, or at least influenced, by definite objects in the visual field, they are usually termed vision. These stages, at least in the examples adduced, must not be taken as representing a genetic series. They shade insensibly into one another, and we have seen how some forms, such as the frog, for example, may give responses which fall into two of the classes. The ordinary responses of the frog to light which enters its eyes fall under what is termed Type C, and to an undetermined extent under Type D. But when the optic nerves are cut, so that the eyes no longer function, the frog still reacts to light, its responses falling under Type A. Can we say that the frog's "sight" has been destroyed then by cutting the optic nerves? It still is responsive to directive light much as it was before. Certainly the commonly accepted usage of the terms "sight"

and "vision" would not cover the responses to light perceived by the integument, and it would perhaps be better to employ for the whole series the terms "photo-reception" and "photo-reaction," which have recently been proposed (see Beer, Bethe u. Uexküll, '99, and Nuel, :04).

Although, as has been said, this classification cannot be taken as representing a genetic series, nevertheless it does indicate in a rough way the steps which have probably led up to the possession of the highest type of vision. The classes as here established are far from distinct, and especially is this true of the last two, which necessarily must depend in part upon each other. However, the form of response outlined under Type C is in general more primitive than that under D. It depends upon a definite phototropic reaction, and as more acute vision is gained phototropism becomes inhibited more and more until it apparently disappears.

No experiments were made to test color perception and its relation to image-formation. This is an extremely difficult field, since it is well-nigh impossible to get an objective criterion as to whether animals perceive color as it is interpreted by the human eye, or whether colors represent to them merely differences in light intensity.

V. SUMMARY.

In the study of the reactions of certain animals to two lights of different areas, the one 41 cm. square, the other only one ten thousandth as much (for all practical purposes a point), the two lights were always adjusted so that they gave an equal intensity of light at a plane midway between them — the plane of experimentation. This intensity varied from about 5 candle meters to 1.25 candle meters. A summary of the principal results obtained is as follows :

1. The earthworm (*Allolobophora foetida*) was negative in its response to either of the two lights used separately ; to the two lights used simultaneously it was indifferent, turning almost exactly as many times in one direction as in the other. *Allolobophora* therefore apparently responds only to the *intensity* of the light.

2. *Bipalium kewense* was similarly negative to either light used singly. To the two lights operating at the same time it was nearly indifferent, but showed a slightly larger number of turnings away from the larger light ; this may indicate a slight ability to discriminate between the lights, and if so, it is probably owing to the arrangement of the eyes around the periphery of the semicircular head.

3. The mealworm (larva of *Tenebrio molitor*) was decidedly negative in its reactions to the lights employed separately. As inferred from its reactions to the two lights acting simultaneously, — the turnings to

and from the large light being equal in number, — its eyes have no ability to form distinguishable images of objects which differ from each other in size no more than did the two lights used.

4. *Oniscus asellus* was found to be negative to light of the intensities mentioned. Its responses to light are not so definite as those of the larva of *Tenebrio*, but there is some evidence that it has a somewhat greater power of discriminating between the two lights acting simultaneously.

5. The cockroach (*Periplaneta americana*) is decidedly negative to light from one side, but the reactions to the two lights used simultaneously showed an almost indifferent condition. The excess of 4.5 per cent of the reactions was on the side of motion toward the larger light, whereas one would have expected that if there were any difference there would have been a predominance of reactions away from the larger light. This is possibly to be explained as due to other disturbing factors.

6. The mourning-cloak butterfly (*Vanessa antiopa*) is uniformly positive in its locomotor reactions to unilateral illumination. Exposed to the simultaneous influence of both lights, it went in 87.2 per cent of its responses toward the larger light, thus confirming Parker's conclusion that this insect responds to the size of the illuminated area rather than to the intensity of the light received from it.

7. *Ranatra fusca* varied in the character of its response to unilateral illumination; but, as far as possible, only positive individuals were employed in the experiments with the two lights used simultaneously. It was found that *Ranatra* gave a somewhat smaller proportion of turnings to the larger light (70.6 per cent) than did *Vanessa*; but it is believed that this may be due to the inconstancy of the phototropic states of *Ranatra*, rather than to less efficiency of the eyes in forming images of the two lights.

Individuals with the posterior half of the eyes blackened went straight ahead, without hesitating, toward whichever light they chanced to face; when the anterior half of the eyes was blackened, they kept turning from one light to the other, since the only one from which light could enter the eyes was always the one behind the insect.

8. The pomace fly (*Drosophila ampelophila*) gave only negative results, owing, apparently, to technical difficulties in the experiments.

9. *Helix pomatia* did not prove to be a good form for the purpose of these experiments, on account of the inconstancy of its phototropic state. So far as the experiments went, they pointed to the conclusion that the eyes are of little or no use in enabling this animal to discriminate between the sizes of the luminous areas employed.

10. *Limax maximus*, on account of the inconstancy of its phototropic responses, was found to be unsuitable for these experiments.

11. The results of the experiments upon the cricket frog (*Acris gryllus*) will be found concisely enumerated on p. 400.

12. The results of the experiments upon the green frog (*Rana clamata*) are enumerated on p. 401.

13. The animals which showed by their reactions the most evidence of discrimination between the two lights (viz., Vanessa, Ranatra, and the two species of frogs) are all positive in their ordinary phototropic responses.

14. The negative animals experimented upon (earthworm, land planarian, mealworm, sow bug, cockroach) showed little or no ability to discriminate between the two areas of illumination, but appeared to respond almost entirely to the intensity of the lights.

15. These reactions are correlated with the natural habits of the animals.

16. There are certain positive forms (especially larvae of Lepidoptera and certain marine Copepoda) which apparently respond to light intensity only; but these are prevented by the conditions under which they live from being brought into unfavorable circumstances by their movements toward the light.

17. The responses of animals to light may be divided roughly into the following types:

Type A. Response of eyeless forms. Usually negative; sometimes positive, and then usually to very weak light. Respond to intensity of light only (e. g., earthworm).

Type B. Response of forms with "direction eyes." Usually negative (e. g., Bipalium, Periplaneta, Tenebrio larva); sometimes positive (e. g., larva of wood-borer), in which case special adaptation prevents their following the light until it brings them into unfavorable conditions. Response almost wholly to intensity of light.

Type C. Response to size of luminous field. Animals usually positive, though they may be temporarily negative, as was seen to be the case with the frog, for example. Probably the response to the size of the field is adaptive only when they are positive.

Type D. Response to definite objects in the visual field. Not simple reactions; responses usually involve psychic phenomena. Respond (1) to moving objects, (2) to stationary objects. This form of response usually inhibits ordinary phototropic reactions.

Types C and D are developed together.

The types outlined above do not necessarily represent a genetic series.

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